APPLYING AN ECOMORPHOLOGICAL FRAMEWORK TO THE STUDY OF ORANGUTAN POSITIONAL BEHAVIOUR AND THE MORPHOLOGICAL VARIATION WITHIN NON-HUMAN APES.

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ABSTRACT

Establishing relationships between morphology and behaviour in response to environmental selection pressures are crucial to understand the evolution of diversity within groups such as the hominoids. Muscle architecture (fascicle length and physiological cross-sectional area) from the fore and hindlimbs in the non-human apes were compared, with the result that it did not differ substantially, likely reflecting their characteristic use of orthograde behaviours. At the micro-architecture level, significant differences in the proportions of fast and slow muscle fibres of the triceps surae were found between orangutans and chimpanzees, reflecting subtle differences in locomotion and habitat use. As the largest, predominantly arboreal ape, orangutans were expected to have specific behavioural adaptations to the complex arboreal habitat. A new method was developed, Sutton Movement Writing and was successfully applied to record the subtle variations in positional behaviour and compliant support use in orangutans under field conditions. Finally, postural specialisations used during feeding in the terminal branch niche were identified. Overall, this thesis shows that although the non-human apes appear to share overall behaviours and morphology, more subtle variations in micro-architecture and behaviour are present in orangutans in response to their habitat, and reflects key adaptations since their split from the last common-ape ancestor.

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1.1 Ecomorphology: the relationship between form and function

The publication of Darwin's 'On the Origin of Species' in 1859 marks the beginnings of our interest in species adaptations in response to the selective pressure of the environment (Bock, 1990). Since then, much of biology has concerned itself with describing and understanding the diversity present and placing it in an evolutionary context, resulting in fields such as functional morphology, evolutionary morphology and ecological physiology (Bock, 1990; Aerts et al., 2002). The way in which an animal functions, taken to mean the roles it must perform in order to survive (i.e. those needed in order to feed, reproduce and avoid predators; Cant, 1992; Gans, 1998) depends on its form (defined here as its anatomical structure). Therefore, in order to understand how an organism is adapted to function successfully and the evolution of the necessary traits, be they morphological or behavioural, we can study the interactions between their morphology, performance and the structure of the habitat utilised (Gomberg et al., 1979; Bock and von Wahlert, 1998). Studies investigating these relationships fall under the heading 'ecomorphology', a term introduced by Karr and James (1975; cited in Bock, 1990), and are primarily concerned with the comparison of different morphological features in relation to their role in the natural environment at different taxonomic levels. Establishing such relationships between form and function in extant species can expand our knowledge of the influences and constraints acting upon them, and thus can provide insight into evolutionary patterns within groups such as the hominoids.

Ecomorphological hypotheses generally assume that differences in morphology produce differences in performance capability, which translate into differences in ecology or behaviour and vice versa (see Garland, 1983; Losos, 1990; Irschick and Garland, 2001). While this can lead to obvious conclusions e.g. a fish has fins to swim in water, there can also be less obvious adaptations that increase the fitness of a species. For example, a species may be adapted to its most frequently performed behaviour e.g humans are adapted for terrestrial bipedal walking and running which is reflected in our foot morphology including features such as enlargement of the calcaneal tuberosity and the presence of the medio-longitudinal arch (Harcourt-Smith and Aiello, 2004; Crompton, et al., 2008). Alternatively, species may be adapted to an infrequently used behaviour that comes under strong selective pressure, for example, tufted capuchin monkeys (*Cebus apella*) show adaptations in their skull and jaw morphology for feeding on particularly tough fallback foods (Wright, 2005). These foods do not form the bulk of their diet, rather they are eaten during periods of food scarcity, but lacking the ability to process them could prove fatal (Wright, 2005; Taylor, 2009). Therefore, it is only by investigating the full repertoire of a species' behaviours that the more subtle adaptations can be understood and the evolution of variation fully explained.

The positional behaviour (i.e. posture and locomotion) of a species is a key component of its ability to survive in its natural habitat. The niche inhabited by a species will be determined by its physical ability to move through and use the habitat and resources present. In order to understand how the phenotypic variation relates to performance, experimental or laboratory studies are necessary to measure maximum capabilities, while studies in the natural environment are required to measure the ecological relevance of a trait (Gomberg et al., 1979; Aerts et al., 2002; Biewener, 2003). The ability to undertake such studies is greatly eased

when measuring steady-state locomotion in terrestrial species, or species that are easy to manipulate and measure in a laboratory setting. For example, there has been a large body of research into the ecomorphological relationships in various species of lizard (e.g. Losos, 1990; Van Damme et al., 2008; Goodman et al., 2008; Clemente et al., 2009; Collar et al., 2010), measuring all components of the morphology-performance-habitat relationship.

These relationships, however, are particularly interesting in challenging environments, such as an arboreal habitat, where the environment is discontinuous and contains flexible supports that will pose many difficulties to the ability of animals to move and maintain postures. The effects of such a habitat will also be exaggerated in an animal of larger body mass. The hominoids, therefore, represent an interesting group to study as species use both terrestrial and arboreal habitats and body mass ranges from 5 kg in gibbons (Vereecke, 2006; Channon et al., 2009) to 200 kg in gorillas (Zihlman and McFarland, 2000). The use of steady-state terrestrial and arboreal locomotor behaviours in these species, such as quadrupedalism, bipedalism and vertical climbing have been relatively well studied (e.g. Larson and Stern, 1987, 2007; Aerts et al., 2000; D'Août et al., 2001, 2002, 2004; Isler and Thorpe, 2003; Isler, 2005), in particular in relation to the evolution of bipedalism in the hominid line (e.g. Prost, 1967; Crompton et al., 2003; Williams, 2010, for a full review see Schmitt, 2003). However, the adaptability and diversity within this group will have also been shaped by their more complex interactions with the arboreal habitat. In particular, the largest, predominantly arboreal ape, the orangutan is known to use un-patterned locomotor gaits to assist its movement through the forest canopy (Thorpe and Crompton, 2005, 2006; Thorpe et al., 2009). These behaviours are more difficult to quantify and study due to their multi-limb, multiple-support use and unpredictable nature, and it is not feasible to study these behaviours in a laboratory setting

due to the difficulties in re-creating the complex arboreal habitat (i.e. multiple, compliant supports at various orientations).

Therefore, field studies need to be developed that are able to record the detailed relationships between positional behaviour and habitat use in such situations to be combined with detailed comparative anatomical data. Overall, by applying an ecomorphological framework to the study of positional behaviour in the extant hominoids, our closest living relatives, we can develop a better understanding of the specialisations undergone by the different species, and thus the evolution of locomotor diversity within this group. This will not only assist in the reconstruction of the behaviours of fossil hominoids, and thus inform us about our own evolutionary history, but it will also provide valuable information to aid in the conservation of the non-human apes, many of which are close to extinction in the wild.

1.1.1 The non-human apes

The apes include the lesser apes (gibbons and siamangs) and the great apes (orangutans, gorillas, bonobos, chimpanzees and humans) and together form the superfamily Hominoidea (see Crompton et al., 2008 for a recent review; Fig. 1.1 for phylogenetic relationships). The family Hylobatidae (the lesser apes) is now considered to consist of four genera (see Roos and Geissmann, 2001): *Hylobates* (gibbon); *Hoolock* (gibbon); *Nomascus* (gibbon) and *Symphalangus* (siamang). The family Hominidae contains four genera, with *Pongo* branching off first, then *Gorilla*, with *Pan* and *Homo* as sister taxa (see Groves, 2001; Chatterjee et al., 2009). At present there are considered to be two species of orangutan (*Pongo pygmaeus* and *Pongo abelii*), with *Pongo pygmaeus* (Bornean orangutan) consisting of three sub-species.

The Sumatran orangutan (*Pongo abelii*) is considered to be one species, although there is growing evidence that it too may divide into different sub-species (Nietlisbach and Krutzen, 2009; Willems et al., 2009). The genus *Gorilla* contains two species (Western gorilla: *Gorilla gorilla* and Eastern gorilla: *Gorilla beringei*), each of which is further divided into two sub-species (Groves, 2003; Taylor and Goldsmith, 2003). The last non-human great ape genus *Pan* consists of two species (Gagneux et al., 1999), *Pan troglodytes* (chimpanzee) and *Pan paniscus* (bonobo), with three subspecies of *Pan troglodytes* (see Groves, 2001). Finally, the remaining genera is Homo, which consists of only one living species, *Homo sapiens*.

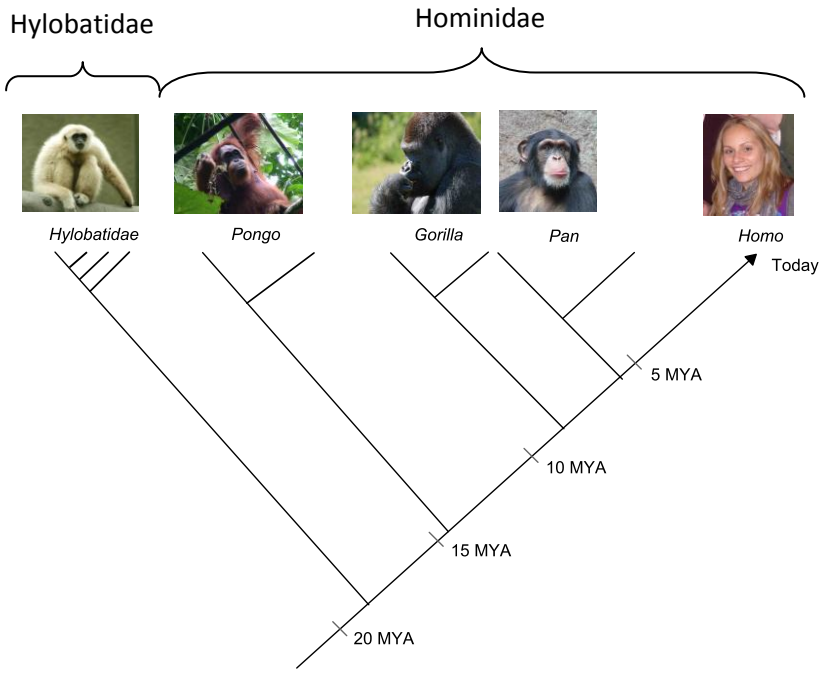

Fig. 1.1. Phylogeny of the superfamily Hominoidea (adapted from Groves, 2001).

Of the non-human apes, the lesser apes, gibbons and siamangs, together with orangutans (the only Asian great ape, found on the islands of Borneo and Sumatra only; see Delgado and van Schaik, 2000) are the Asian apes. The great apes, gorillas, bonobos and chimpanzees are found in the central tropical region of the African continent only, while humans have now spread to in-habitat every continent of the world. A wide range of body masses are found within the apes and there is also a large amount of sexual dimorphism in some species, such as orangutans, where the females weigh 35 kg on average, and the males average 86 kg (Markham and Groves, 1990). Although all of the non-human apes are arboreal to some extent, the proportion of time spent in the forest canopy differs across the species. The Asian apes are the most arboreal, spending nearly all of their time in the canopy, although flanged adult male Bornean orangutans will travel on the ground (see Galdikas, 1988). The African

apes enter the forest canopy in order to feed, but they often spend a greater proportion of time travelling and socialising terrestrially (e.g. Hunt, 1992a, b; Doran, 1993a, b; Remis, 1995; Fleagle, 1999). Despite their differences, all the apes share a number of common features, both morphologically and behaviourally, such as their morphological adaptations in the forelimb to their shared use of suspensory behaviours (Larson, 1998; Ward, 2007). By undertaking detailed studies of their structure and performance in their arboreal habitat we can develop a better understanding of the influences and constraints that have resulted in both their shared and also their specialised adaptations to their different niches.

1.2 The study of form: functional morphology in the non-human apes

In order to understand the form of an animal we need to undertake anatomical investigations, taking functionally relevant measurements which in turn be related to the function of an animal and its performance in a natural setting. The musculo-skeletal system is controlled by the nervous system and functions by enabling the generation and transmission of the forces that control the movement of the body (Watkins, 2009). The muscles themselves generate the forces that are transmitted to the bones of the skeleton which act as a lever system to transfer forces to the joints to enable movement (Nigg and Grimston, 1994; Watkins, 2009). Muscles are attached to the bone either via aponeurosis or tendons which may be present at only one or both ends of a muscle and can be both external to the muscle belly, and also run through the muscle belly itself (Elliot, 1965; Ker et al., 1988).

At the smallest level, the muscles themselves consist of sarcomeres, which contain the two contractile proteins or filaments, actin (thin filament) and myosin (thick filament), among

others (Ganong, 2001). Repeating units of sarcomeres, separated by Z lines, together form a myofibril, and bundles of parallel myofibrils form what is referred to as a muscle fibre. The individual muscle fibres are the 'building blocks' of muscle and exist in different forms, or fibre types, which differ in their contractile speed, amongst other properties (Woledge et al., 1985). Muscle fibres group together in bundles (called muscle fascicles) and are bound together by connective material to form the belly of the muscle (Ganong, 2001). A group of muscle fibres innervated by a single motoneuron is the most basic functional unit of a muscle, referred to as a motor unit, which consists of fibres of only one type (see Monti et al., 2001). The number of fibres within a motor unit can vary depending on the function of the muscle e.g. for fine motor control such as the movement of the eye one motor unit consists of only 3-6 fibres, whereas leg muscles may have hundreds of muscle fibres to a motor unit (Ganong, 2001). The muscle fibres attach themselves to the bone via either a tendon or aponeurosis in order to transmit the forces generated to the skeleton to enable movement (see Figure 1.2 for an overview of muscle structure).

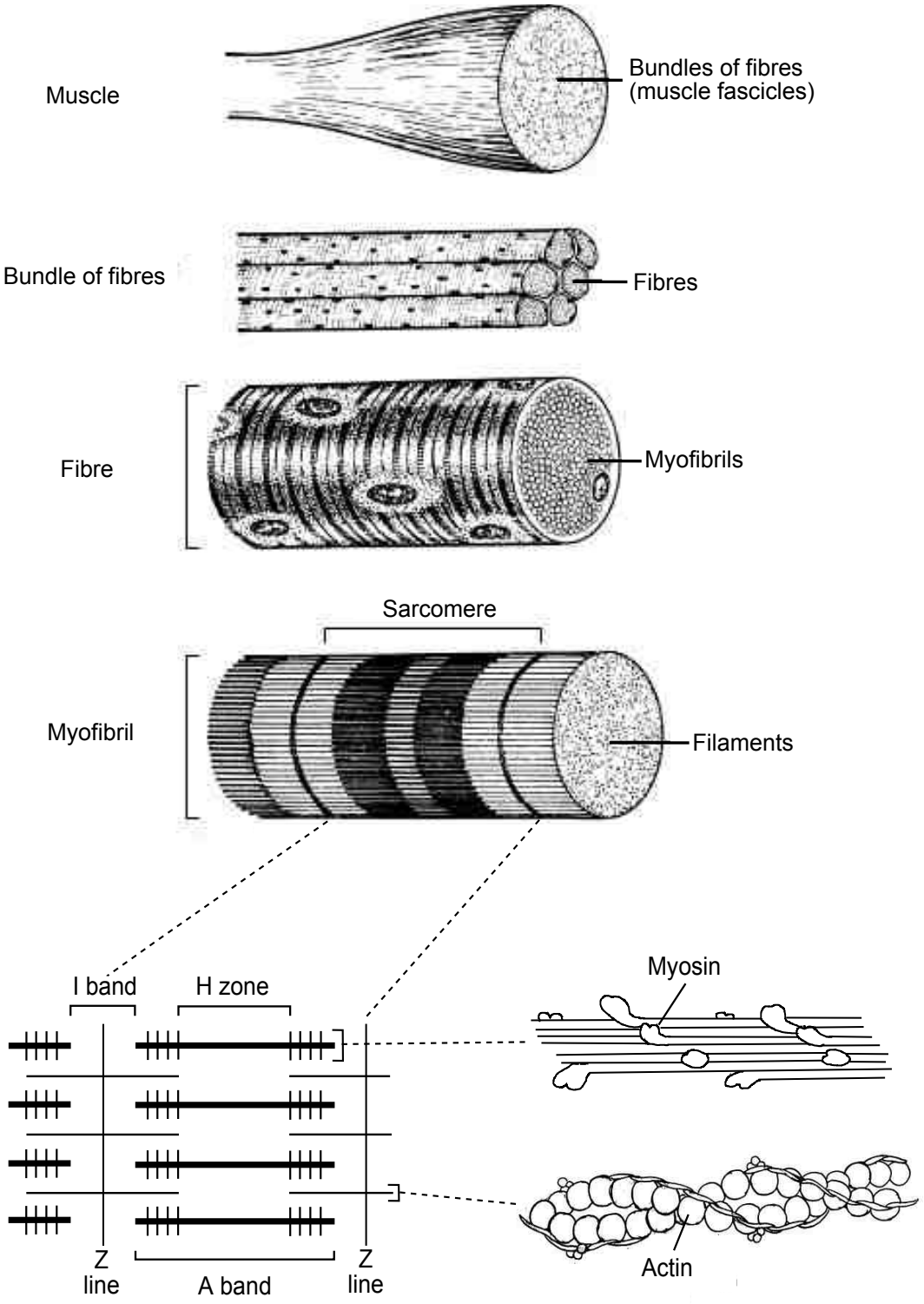

Figure. 1.2. Hierarchy of muscle structure (adapted from Jennett, 1989)

1.2.1 Muscle macro-architecture

Five parameters of the gross anatomy of muscle-tendon units (MTU) have been highlighted as key in determining the functional capabilities of a muscle (Zajac, 1992); these are the physiological cross-sectional area (PCSA) of a muscle, the length of the muscle fascicles, the angle of pennation (the angle of the muscle fibres to the point of insertion), the length and properties of the tendon and the muscle moment arm (Fig. 1.3 shows an outline of some of the basic measurements taken from the muscle-tendon unit).

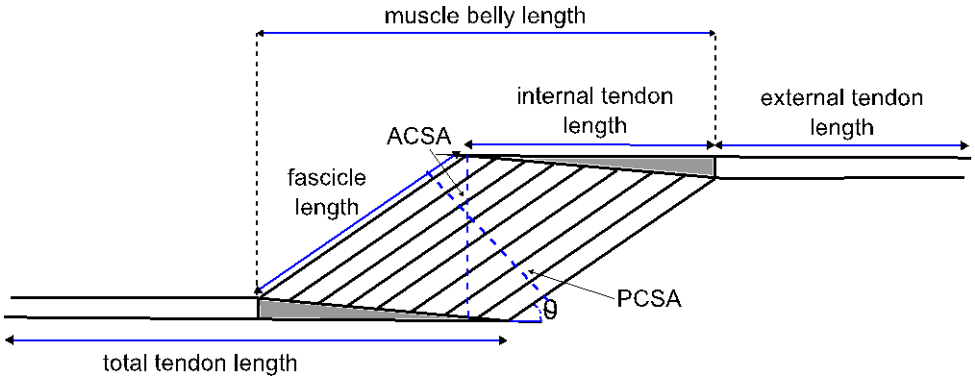

Fig. 1.3. Diagrammatic interpretation of a muscle-tendon unit adapted from Zajac (1992). The muscle belly contains muscle fibres that lie parallel to each other (fascicle length), although they insert onto the internal tendon/aponeurosis at an angle (θ), which is greater than 0^o, thus the muscle in this diagram is pennate in structure. ACSA refers to the actual cross-sectional area of the muscle, PCSA refers to the physiological cross-sectional area. This muscle has both internal and external tendons.

The fibres themselves, and thus the muscle form, can be described as either parallel or pennate (Herzog, 1994). In parallel muscles the fibres run through the muscle belly, following the line of

action. When the muscle fibres run at an angle to the line of action they are referred to as pennate (see example in Fig. 1.3). The actual cross-sectional area of a muscle (ACSA; Fig. 1.3) varies depending on whether a muscle is parallel or pennate fibred, as in pennate muscle ACSA will not cross all of the fibres at a right angle, therefore physiological cross-sectional area (PCSA; Fig. 1.3) is used when measuring muscle cross-sectional area to take this into account (see Zajac, 1992). PCSA reflects the number of sarcomeres in parallel, and provides an indication of the maximum force a muscle can produce because force is proportional to area (Sacks and Roy, 1982; Zajac, 1992). Muscle fascicle length (as a measure of muscle fibre length), however, reflects the number of sarcomeres in series and the longer the fascicle length, the greater the maximum shortening velocity of the muscle fascicles and the range of motion at the joint (see Wickiewicz et al., 1984; Zajac, 1992; Thorpe et al., 1999). Therefore, depending on the function of a muscle it will range from an optimal 'in parallel' arrangement to maximise force generation, or an optimal 'in series' arrangement of fibres to maximise speed and excursion (Wickiewicz et al., 1984; Thorpe et al., 1999). The angle of pennation (i.e. the angle at which the muscle fibres insert on the aponeurosis or tendon) additionally affects the force producing capacity of a MTU and can be included in the calculation of PCSA (Alexander and Vernon, 1975; Zajac, 1992). As pennation angle decreases along the line of action (see Figure 1.3), the capacity of a muscle to produce force decreases, but its capacity for speed increases, however, these effects only become significant when the pennation angle is greater than approximately 20 degrees (Zajac, 1992).

Tendons are able to stretch and store elastic strain energy when a muscle contracts, which is subsequently recovered when the muscle unloads (e.g. Alexander, 1984, 1991, 2002; Bennett et al., 1986; Azizi and Roberts, 2009). Therefore, the presence/absence of a tendon and its properties can significantly impact on the functional abilities of an MTU. Elastic energy storage is an important energy saving mechanism in gaits such as running or hopping and tendons in such situations are able to store and return over 90% of the internal kinetic energy that would otherwise by lost (Ker, 1981; Ker et al., 1988., Alexander, 1991; Pollock and Shadwick, 1994). Aponeuroses is also made up of collagen fibres and can create a direct connection to the bone when there is no external tendon, or form a sheet-like arrangement across the muscle belly leading from the tendon. These aponeurotic structures can also behave like springs during locomotion, and may also play a role in energy saving mechanisms (Azizi et al., 2009). To ascertain the capacity of a tendon to store elastic energy during locomotion tendon stress can be calculated (force/cross-sectional area), with a high value of tendon stress indicating that the tendon will be stretched more during locomotion and is therefore more likely to act as an energy store (Ker et al., 1988; Alexander, 1991; Ker et al., 2000). The final measure of muscle function obtainable from anatomical dissection is its moment arm. The moment arm of a muscle is the shortest perpendicular distance from the MTU to the joint centre of rotation and is the variable that informs us of the capability of a muscle to transfer the linear properties into rotational ones about a joint e.g. muscle force into moment of muscle force and muscle speed into angular speed (Zajac, 1992).

1.2.2 Macro-architecture in the non-human apes

Although, the measurements required to assess the functional capabilities of an MTU are relatively simple, the study of functional muscle architecture in the non-human apes only really began at the end of the last decade (Thorpe et al., 1999). Thorpe and colleagues (1999) measured muscle belly mass, fascicle length and PCSA together with flexion/extension moment arms in the fore and hindlimbs of three chimpanzees. Once scaled to take differences in body mass into account, they compared these data to previously published data of human muscle architecture. The results indicated an adaptation for mobility over force production in the hindlimb muscles of chimpanzees, the reverse to the situation found in human hindlimbs, relating to the use of arboreal behaviours in chimpanzees. In the forelimb the chimpanzees had both greater PCSAs and longer fascicle lengths compared to humans, due to their increased use of forelimb dominated behaviours compared to humans (Thorpe et al., 1999). The study of ape anatomy, however, is certainly not new, with the first study of an infant chimpanzee published in 1699 (Tyson, 1699). In spite of this long history, studies of ape locomotor anatomy remained fundamentally descriptive (e.g. Owen, 1859; Sonntag, 1923, 1924; Miller, 1952; Ashton and Oxnard, 1962a, b; Sigmon, 1974; Swindler and Wood, 1973; Sigmon and Farslow, 1986; Langdon, 1990; see Gibbs et al., 2002 for a full review) until the last decade, with interpretation of muscle function limited to descriptions of origins and insertions, relative sizes and differences in overall structure e.g. the number of muscle heads and muscle fascicle direction (e.g. Ashton and Oxnard, 1962a, b).

Since Thorpe et al's (1999) study, a number of studies of the functional anatomy (both muscle architecture and moment arm data) of the locomotor muscles (hindlimbs and forelimbs) in the non-human apes have been carried out. Data have now been obtained from chimpanzees (fore and hindlimb muscle architecture and moment arms: Thorpe et al., 1999; Carlson, 2006; forelimb architecture: Oishi et al., 2009; Kikuchi, 2010; hindlimb muscle architecture and moment arms: Payne et al., 2006a, b); bonobos (hindlimb muscle architecture and moment arms: Vereecke et al., 2005; Payne et al., 2006a, b); gorillas (hindlimb muscle architecture and moment arms: Payne et al., 2006a, b); orangutans (hindlimb muscle architecture and moment arms: Payne et al., 2006a, b; forelimb muscle architecture: Oishi et al., 2008, 2009) and gibbons (hindlimb muscle architecture: Vereecke et al., 2005; Payne et al., 2006a; Channon et al., 2009; hindlimb moment arms: Payne et al., 2006b; Channon et al., 2010; forelimb muscle architecture: Michilsens et al., 2009; Kikuchi, 2010). However, the majority of these studies obtained data from only a small number of individuals from one or a few species in any one study. Furthermore, due to interest in the evolution of hominin bipedalism, to date, studies of ape muscle architecture have frequently focused on hindlimb anatomy (e.g. Thorpe et al., 1999; Carlson, 2006; Payne et al., 2006; Channon et al., 2009) with forelimb muscle architecture being studied to a lesser extent and in fewer species (e.g. chimpanzee: Thorpe et al., 1999; Carlson, 2006; orangutan and chimpanzee: Oishi et al., 2008, 2009; gibbon: Michilsens et al., 2009), with no data for bonobos or gorillas yet available. Despite their differences in habitat and positional behaviour, however, the apes are considered to be united predominantly by their shared features in the upper limb, such as short, stiff lumbar spines, broad ilia, broad, shallow trunks, dorsally placed scapula, and shoulder joints adapted for highly abducted arm postures (e.g. Larson, 1998; Ward, 2007; see Fig. 1.4).

Therefore, forelimb studies are also crucial, and by relating the measurements of muscle architecture (anatomical form) from both the fore and hindlimbs, to the behaviours performed by the animal (the function), we can further explore whether subtle differences in non-human ape adaptations to their habitats exist, in addition to their shared features.

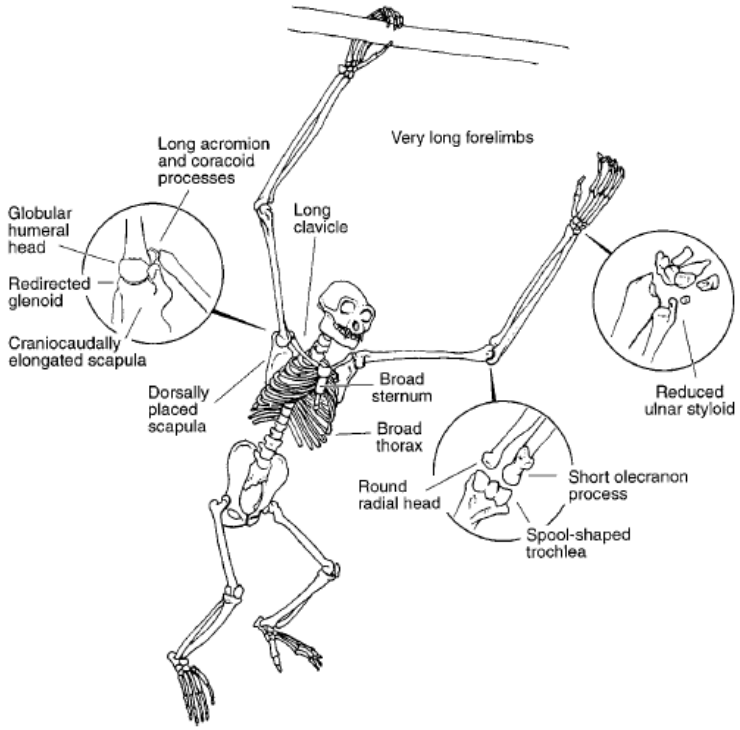

Fig. 1.4. Shared commonalities in the morphology of the apes (taken from Larson et al., 1998).

Previous studies of ape muscle architecture have generally shown what was expected, that differences in locomotor behaviour are reflected in the muscle architecture of the species, for example, gibbons have more powerful elbow flexors linked to their use during brachiation, compared to non-specialised brachiators (Michilsens et al., 2009). Differences between species have been identified with the non-human apes having longer muscle fibres in their hindlimbs compared to humans, which is most likely related to their need to produce force over a greater

range of motion in their arboreal habitat compared to humans who need to produce greater forces over a smaller range of motion during terrestrial bipedalism (see Thorpe et al., 1999; Payne et al., 2006a, b). Oishi et al (2009) also identified specific differences between chimpanzees and orangutans in their forelimb muscles with orangutans having increased force production ability (larger PCSAs) in their elbow flexors, which they related to the increased use of arboreal suspensory locomotion in orangutans compared to chimpanzees. There are, however, fewer moment arm data available from the non-human apes (Thorpe et al., 1999; Payne et al., 2006; Channon et al., 2010). Both sides of a cadaver are required to collect moment arm data, as it cannot be collected from the same limb as the muscle architecture, due to the different cuts that need to be made in the muscle belly. Both sides, however, are not always available for dissection due to their use in other studies, thus reducing the moment arm data available. From the studies undertaken, Thorpe et al. (1999) found that chimpanzees were adapted for a considerably greater range of movement than humans in both their fore and hindlimbs, which concurs with the muscle architecture data that chimpanzees need to be able to produce force over a range of joint positions (Thorpe et al., 1999). A similar result was also found for the hindlimb moment arms in a range of non-human apes species in comparison to humans (Payne et al., 2006b) and in a separate study of gibbon hindlimbs (Channon et al., 2010).

However, comparing data and making firm conclusions from these different studies is problematic, partly because of the small sample sizes and partly because of the variation in collection methods. Ape cadavers are difficult to obtain as studies are performed on apes that die

naturally in captive conditions. Therefore, it can take many years to build up a suitable sample size, and samples often contain of a mixture of age-sex classes in one study. Individual variation, even between animals of the same age-sex class, may also be high due to different captive conditions and activity levels of individuals, for example, in humans an increased amount of inactivity results in a decrease in muscle volume and PCSA (e.g. Kawakami et al., 2000). Combining data from different studies for comparison is often impractical due to the variation in the cadaver material i.e. fixed or fresh, and the techniques used to record the data. Particularly problematic is the comparison of data from fresh-frozen tissue with either formalin or formaldehyde fixed material. Muscle fixation, particularly after removal from the bone (as used by Oishi et al., 2008, 2009) results in fibre shrinkage (Cutts, 1988). Furthermore, the density of fixed muscle varies to that of fresh muscle (Ward and Lieber, 2005), and therefore the calculation of PCSA should be modified to take this into account before comparison, a fact often missed (e.g. Carlson, 2006; Oishi et al., 2008, 2009; Kikuchi, 2010). Studies also vary in their methods used to record the measurements, for example, Carlson (2006) attempted to compare his data collected using re-hydrated weight from previously dried, fixed material to wet weight from fresh material (Thorpe et al., 1999). Attempting to correct for these differences in material condition and collection method is likely to add further errors into data sets that already suffer from a large amount of variation e.g. due to variations in age-sex class or captive conditions, therefore comparison between different species should ideally be reserved for data collected using the same method, from material in the same state. Therefore, Payne et al's (2006a, b) hindlimb study is the only truly comparable data set from all the apes, as although they included an alcohol fixed

orangutan in the general description, these data were removed for the scaled comparison resulting in a direct comparison of fresh data only.

Comparing the muscle architecture of the non-human apes, is complicated further by the large differences in body mass between the different species and age-sex classes which needs to be removed or taken into account before the variation due to differences in locomotor behaviour can be assessed. To date, previous studies have often use a form of scaling to normalise the data, either dividing the muscle parameter (e.g. muscle belly mass, fascicle length and PCSA) by a measure of body size e.g. body or limb mass (body-mass ratios e.g. Oishi et al., 2008, 2009) or by geometric scaling (e.g. Thorpe et al., 1999; Payne et al., 2006a; Channon et al., 2009, Michilsens et al., 2009). Two animals are considered geometrically (or isometrically) similar if one can be made identical to the other by multiplying all length dimensions by the same factor (Alexander, 2000). If animals were geometrically similar, the masses would be proportional to $(mass)^{1}$, lengths to $(mass)^{1/3}$ and areas to $(mass)^{2/3}$, and plotting the variable of interest (e.g. muscle PCSA) against a measure of body size (e.g. body mass) would result in a straight line passing through the origin (see Schmidt-Nielson, 1984; Packard and Boardman, 1987; see Fig 1.5).

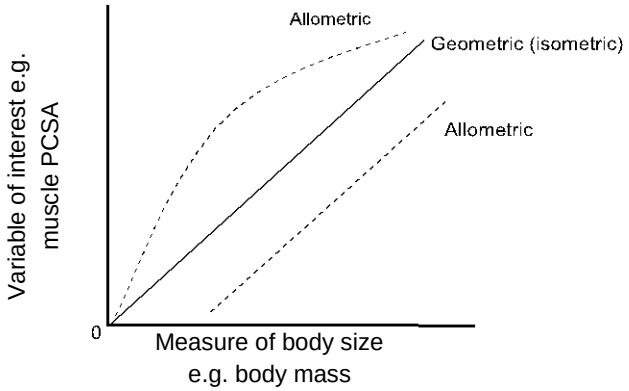

Fig. 1.5. Comparison of morphological data plotted against body mass showing the different scaling relationships (adapted from Packard and Boardman, 1987).

In reality, however, a plot of the variable of interest against body mass more often results in a linear relationship that does not pass through the origin, or a curvilinear relationship, and is described as allometric, where the variable does not alter in direct proportion to body mass (see Smith, 1984; Packard and Boardman, 1987; Brown et al., 2000; Biewener, 2003). This is often due to variations during ontogeny or evolution, and adaptations to different lifestyles (see Alexander et al., 1981; Nevill et al., 2005). The use of geometric scaling, therefore, may not actually be the most appropriate method by which to scale and compare anatomical data from different species. Therefore, the use of allometric scaling methods or alternative statistical analysis to obtain a more reliable conclusion as to the functional differences present is required to obtain a more robust comparison of the different species.

1.2.3 Muscle micro-architecture

The properties ascertained from macro-architecture, however, are not the only ones to impact on muscle function. The muscle fibres themselves consist of a variety of types that differ in their mechanical, biochemical and energetic behaviour, thus further influencing the function of a muscle (Woledge et al., 1985; reviewed by Pette and Staron, 1990; Scott, 2001). Muscle fibres can be classified into different types based on their various properties (see Monti et al., 2001 for a review). Based on physiological properties, muscle fibres can be divided into fast and slow (Burke et al., 1971). Further division is possible, based on the properties of the contractile protein myosin, which consists of both heavy and light chains. The myosin heavy chain (MHC) exists in different isoforms and it is the presence of the different isoforms that largely determines the contractile speed of a muscle fibre (see Bárány, 1967; Close, 1967). Further analysis of the fibre's metabolic pathway based on myosin ATPase histochemistry reveals two types of pathway, either aerobic/oxidative or anaerobic/glycolytic (Peter et al., 1972). Combining these properties results in muscle fibres being defined as either fast (type IIa and IIb), also known as FOG (fast oxidative glycolytic) and FG (fast glycolytic) fibres respectively or slow (type I), also known as SO (slow oxidative) fibres. Slow fibres are slow contracting, but fatigue resistant in comparison to fast fibres which are fast to contract, but quick to fatigue. Further fibre subtypes have been identified that may differ between muscles or species (see Punkt, 2002) e.g. a superfast $MHCII_m$ isoform has been identified in masticatory muscle (Pette and Staron, 2000), but functionally the division of the muscle fibres into fast and slow is the most relevant to studies of locomotor behaviour. The proportion of the different muscle fibre types can vary within an individual muscle, thus further altering the properties of the muscle. Functionally, the different proportions

of fibre types do not influence the amount of force that a muscle can produce as all fibre types produce the same amount of force, rather it is the speed with which the force can be produced and the length of time that it can be maintained for that varies and can impact on locomotor performance (Zierath and Hawley, 2004).

During locomotion, or when a muscle is activated, slow fibres are recruited first as they are the slowest to fatigue, fast fibres are generally only recruited for movements that require greater speed of movement (Ganong, 2001; Monti et al., 2001). Muscles with a high proportion of slow fibres tend to be predominantly used in anti-gravity, postural or endurance roles, whereas muscles with a high proportion of fast fibres are important for powerful, propulsive movements, such as jumping or sprinting in addition to quick responses and counterbalancing movements, such as those needed during dynamic stabilisation (e.g. Sickles and Pinkstaff, 1981b; Rome et al., 1988; Schilling, 2009). In addition to a muscle having an overall proportion of fast and slow fibres, particular fibre types may also be segregated into specific regions (reviewed by Kernell, 1998). Functionally, such fibre type regionalisation has been linked to the maintenance of joint stabilisation, energy-saving mechanisms and improved muscle efficiency (see Kernell, 1998; von Mering and Fischer, 1999). For example, a recent study by Lucas-Ozma and Collazos-Castro (2009) identified different fibre types in the three heads of the triceps surae muscle of rats, with the lateral head containing predominantly type IIb fibres, the medial head contained mainly type I fibres and the lateral head a mixture of all types. Functionally, this enables an animal to respond

more efficiently to the different tasks they may face in a varied environment and, depending on the specific role required, either all three heads can be used together or separately.

Regionalisation, however, can be even more specific, occurring within a single muscle head (e.g. Wang and Kernell, 2000; Dahmane et al., 2005). In Wang and Kernell's (2000) study they assessed the proportion of type I fibres at seven points along the proximo-distal axis of several hindlimb muscles in rats (see Fig. 1.6. for an example). In these muscles there was a decrease in the proportion of type I fibres from the proximal to the distal end of the muscle belly, possibly related to heat-enhancement to increase muscle power in proximally situated slow fibres (Wang and Kernell, 2000). Functionally, such fibre type regionalisation has been linked to the maintenance of joint stabilisation, energy-saving mechanisms and improving muscle efficiency (see Kernell, 1998; von Mering and Fischer, 1999). Studies such as this (Wang and Kernell, 2000), however, have rarely been undertaken, with studies often using data obtained from one cross-section or a small number of biopsies (e.g. Ariano et al., 1973; Sickles and Pinkstaff, 1981a, b; Rice et al. 1988; Williams et al., 1997; Kimura, 2002; Srinivasan et al., 2007), as this is often the only method available when obtaining data from live animals. As the number of studies demonstrating the regionalisation of muscle fibre types increases (e.g. Gardiner et al., 1991; Kernell, 1998; Punkt et al., 1998; von Mering and Fischer, 1999; Wang and Kernell; 2000; Dahmane et al., 2005; Moritz et al., 2007; Schmidt and Schilling, 2007) however, the importance of studying fibre type distribution throughout the entire muscle belly is highlighted, and studies

should at least take into account the fact that it may vary when investigating functional specialisations.

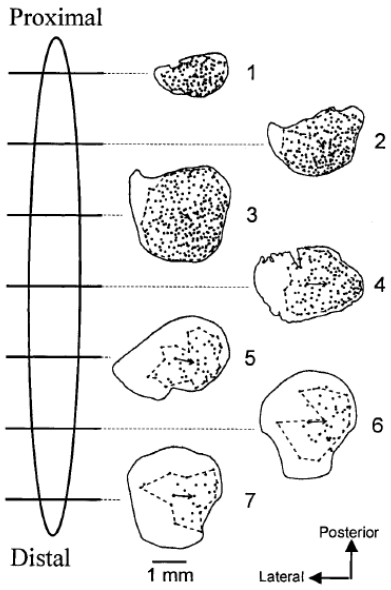

Figure. 1.6. Diagram showing the varied distribution of slow fibres (black dots) throughout the muscle belly of rat extensor digitorum longus muscle, showing a decrease in slow fibres towards the distal end (taken from Wang and Kernell, 2000).

A further factor that should be taken into account when studying muscle fibre types in locomotor muscles is the plastic nature of muscle fibres and their ability to change their properties. Factors that may result in fibres changing 'type', or fibre atrophy (shrinkage) include re-innervation (see Pereira et al., 2010 for a recent example), mechanical loading/unloading (e.g. Loughna et al., 1990), exercise (although these changes are generally restricted to changes within the fast sub-types unless very intense exercise is undertaken; see Green et al., 1979; Demirel et al., 1999), hormonal changes (e.g. Vadazsova et al., 2006) and aging (Porter et al., 1995; Roos et al., 1997).

These possible changes therefore need to be taken into consideration when studying muscle fibre types. Furthermore, while fibre type proportion does influence the function of the muscle, other features such as macro-architecture and maximal oxygen uptake ability also need to be taken into account when determining how well an individual will perform at a particular task (e.g. Zierath and Hawley, 2004).

1.2.4 Muscle micro-architecture in the non-human apes

The relationship between fibre type composition and locomotor behaviour has been relatively well-documented in a range of animals (e.g. cheetah: Williams et al., 1997; ferret: Moritz et al., 2007; mouse: Hesse et al. 2010; rat and rabbit: Fuentes et al., 1998; tree shrew, cotton top tamarind and squirrel monkey: Schmitt and Schilling, 2007). The fibre type composition in the fore and hindlimb muscle of primates has also been studied in some detail (e.g. Sickles and Pinkstaff, 1981a, b; Anaopol and Jungers, 1986; Acosta and Roy, 1987; Petter and Jouffroy, 1993; Jouffroy et al., 1999; Singh et al., 2002; Anapol and Gray, 2003; Schmidt and Schilling, 2007), but studies of non-human ape fibre type proportions are greatly lacking. In fact, to date, only two studies by Kimura (1992, 2002) have been published. Kimura (1992) compared the muscle fibre types in the biceps brachii muscle of crab-eating macaques and white-handed gibbons. The arboreal, brachiating gibbon had more slow fibres relating to its need to bear body weight in suspension compared to the macaque, a terrestrial quadruped, requiring more speed for propulsion (Kimura, 1992). In the 2002 study, Kimura again compared the composition of muscle fibre types, this time in the psoas major muscle of humans, orangutans and monkeys. The

frequency of type II fibres was lowest in the humans, intermediate in the monkeys (baboons and macaques) and highest in the orangutans. This larger proportion of fast fibres in the orangutan was linked to the need for powerful and acrobatic hip flexion when moving its large body mass through in its arboreal habitat (Kimura, 2002).

Caution should nevertheless be taken when interpreting fibre typing data from the non-human apes, as data are usually obtained from captive animals and their locomotor repertoires can often differ to those of wild animals, although as enclosures become better designed captive and wild repertoires are becoming more similar (e.g. Hanson et al., in prep). Depending on the severity of these differences, and differences in activity level between individuals, this may result in variable muscle fibre type distributions due to the plastic nature of muscle fibres, similar to that observed in humans with different activity levels (e.g. Green et al., 1979; Demirel, 1999). However, a substantial difference is required (e.g. complete inactivity for a period of days) to change fibres from fast to slow and vice versa (e.g. Loughna et al., 1990), as the changes are more often within a single overall type i.e. from fast type IIa to fast type IIb. Furthermore, a study by Williams et al. (1997) found that the fibre typing profiles from wild and captive cheetah were remarkably similar, supporting the use of captive animals for these studies. Overall, the use of muscle fibre typing is a greatly under-used technique for studies of non-human ape morphology and yet it is only by combining this detail with measurements of macro-architecture that we can truly understand the subtle ways in which the non-human apes are adapted to their varying habitats and behaviours.

1.3 The study of function: locomotion and posture in the non-human apes and the use of arboreal habitats

1.3.1 Measuring locomotion in the laboratory

Understanding how phenotypic form, as ascertained from studies of morphology, is related to function, requires study of the locomotion and behaviour of the animal. Measures of non-human ape performance can be recorded in laboratory situations to obtain specific measurements and details of maximal performance e.g. electromyographical (EMG) measurements (e.g. Tuttle et al., 1979, 1983; Tuttle and Basmajian, 1978; Stern and Susman, 1981; Larson and Stern, 1986, 1987; Stern and Larson, 2001), kinetics (e.g. Chang et al., 1997; Vereecke et al., 2006a, b; Schoonaert et al., 2006; Wunderlich and Jungers, 2009) and kinematics (e.g. Aerts et al., 2000; Bertram and Chang, 2001; Isler and Thorpe, 2003; D'Août et al., 2004; Isler, 2005; Vereecke et al., 2006). These methods can inform us explicitly about muscle activation patterns during particular behaviours (e.g. EMG of gluteal muscles in gibbons, orangutans and chimpanzees during terrestrial behaviours; Stern and Susman, 1981), the forces and pressures involved (e.g. the reaction forces and moments during brachiation in gibbons; Chang et al., 2007) and the gait patterns and positions of limb segments during locomotion (e.g. comparison of the joint angles and limb range of motion during vertical climbing in the non-human apes; Isler, 2005).

However, undertaking studies of this nature are often difficult as they generally have to be performed in laboratory or captive conditions, although Isler and Thorpe (2003) did incorporate kinematic data from animals in the wild; are generally limited to a small number of individuals;

and are focused on a few key locomotor behaviours that can be recorded with relative ease in captive conditions e.g. terrestrial quadrupedalism and bipedalism (see Prost, 1967; Jenkins, 1972; Yamazaki and Ishida, 1984; Aerts et al., 2000; D'Août et al., 2002; Vereecke et al., 2005b, 2006a, b and c). Their use, therefore, is limited when a range of behaviours are of interest, or the behaviour or habitat itself are complex e.g. arboreal environments. Although a number of studies have attempted to recreate aspects of arboreal habitats using poles (e.g. Chang et al., 1997; Schmitt, 1999; Bertram and Chang, 2001; Schmitt and Lemelin, 2004; Hanna et al., 2006; Schoonaert et al., 2006), it is difficult to truly represent such a habitat. In particular, the flexible (compliant) nature of arboreal supports is especially difficult to recreate, but has a critical influence on the positional behaviours employed by arboreal primates (e.g. Cant, 1992, 1994). Demes et al (1995, 1999) created a compliant force pole to study the take-off and landing forces in Malagasy vertical clingers and leapers, although this system was limited to a very specific behaviour and a relatively manageable species. Therefore, although a combination of both laboratory and field studies to obtain the full overview of an animal's performance capabilities is the ideal situation, it is often not possible, and the collection of detailed, quantitative field data to enable comparison of the more complex positional behaviours in a natural habitat in relation to their morphology is desirable.

1.3.2 Locomotion and posture in the field: the study of non-human ape positional behaviour

Not every movement that occurs in the positional behaviour repertoire of a species will result in morphological changes, rather, those behaviours that encounter the greatest stresses, or sub-maximal stresses regularly, over a long period of time, will be the ones most likely to result in modifications (Preuschoft, 1979; Hunt, 1991, 1996). These may be experienced during the most frequently used behaviours, or during rare behaviours that are key to survival e.g. leaping to escape from a predator. Muscle tissue, tendons and bones need to be adapted to cope with the stresses experienced during all the behaviours occurring in an animal's locomotor repertoire because a sudden jump, or movement exceeding such a threshold would result in the failure of that structure, which could be fatal for the animal (Preuschoft, 1979; Biewener, 2003). Therefore, a full understanding of the entire locomotor repertoire of a species is required before this knowledge can be applied to its morphological form.

The first field studies of the non-human apes generally described their locomotor and postural behaviours in broad terms, often grouped as part of a larger study of their overall behaviour (e.g. Clark, 1959; Schaller and Emilen, 1963; Fleagle, 1999; Rijksen, 1978), thus providing only a general interpretation of their functional capabilities. Prost (1965), however, aimed to rectify this by providing a system by which positional behaviour (locomotion and posture) could be defined and compared between species more accurately. Locomotion was defined as the transition from one place to another and posture as the alternative state, whereby only minor readjustments of

body parts occur, but these can also ultimately result in changes to the spatial placement of body mass (Prost, 1965).

Prost (1965) was the first to highlight the need for a standardised, robust system by which to compare the positional behaviour of primates. Hunt and colleagues (1996) further refined this system by defining behaviours based on kinematic differences, breaking them down into biomechanically distinct modes and sub-modes based on their main weight-bearing body parts, the method of weight-bearing (e.g. in suspension or compression) and torso orientation. Studies of positional behaviour obtaining this detail enable questions to be asked about how animals are adapted to their specific environments and how they are able to perform key behaviours inherent to their survival. Wild chimpanzees were studied in considerable detail during the nineties and over the last decade (see Hunt, 1991a, b, 1992a, b, 1994, 1996; Doran, 1992, 1993a, b; Stanford, 2002, 2006; Pontzer and Wrangham, 2004), partly due to their particularly close evolutionary relationship to humans and theories surrounding the evolution of bipedalism in the hominins. However, the positional behaviour of bonobos has been relatively under-studied, with only one comparative study of bonobos and chimpanzees published (Doran, 1993a). Few data are also available for gorillas, with only two studies of lowland gorilla positional behaviour (Remis, 1995, 1999) and one comparative study of the ontogeny of locomotion in gorillas and chimpanzees (Doran, 1997). Data are lacking for bonobos and gorillas predominantly because of the political climate in the countries where these species are found, thus restricting access to researchers. As a group, however, the African apes are characterised by their use of terrestrial knuckle-walking

locomotion, a quadrupedal locomotor mode where the weight of the forelimbs is borne on the knuckles, rather than the palms or fists as observed in other primates (Hunt, 1991, 1992a, b; Doran, 1993a, b; Remis, 1995). Whether this behaviour evolved independently or in a common ancestor of *Pan* and *Gorilla*, however, remains an ongoing discussion due to some evidence that there are kinematic differences between the two (Dainton and Macho, 1999; Kivell and Schmitt, 2009; Williams, 2010).

Of the Asian apes, wild gibbon and siamang positional behaviour has rarely been studied in detail, although Fleagle (1976) studied siamang positional behaviour and Cannon and Leighton (1994) compared the gap crossing strategies and the use of supports in gibbons and macaques. More recently, Nowak and Reichard (2008) have presented data on the positional behaviour repertoire of white-handed gibbons (*Hylobates lar*), although this has yet to be published. Gibbon locomotion appears to be characterised by their use of brachiation (below-branch suspensory arm-swinging; Hunt et al., 1996), and while the other apes also use brachiation, gibbons are the only true brachiators that use a ricochetal form to move rapidly through the canopy (Bertram, 2004).

The first studies of orangutan positional behaviour were undertaken in the late eighties by Sugardjito (1982), Sugardjito and van Hooff (1986) and Cant (1987a, b). However, Sugardjito and van Hooff (1986) used only broad categories to classify the behaviours observed, identifying only four postures and five locomotor modes. Furthermore, data were only obtained during

resting and travel and not during feeding (Sugardjito and van Hooff, 1986), a key component of an orangutans daily activity (range from approximately 33 to 62% of daily activity; see Morrogh-Bernard et al., 2009). Cant (1987a, b) focused, firstly on postural differences between adult males and adult females during feeding and secondly, the range of positional behaviours observed in adult females. No further field studies were then undertaken on orangutan positional behaviour until Thorpe and Crompton's (2005) detailed assessment of the complete locomotor repertoire of Sumatran orangutans and habitat use which incorporated study of the diameter, type and number of the supports used, height in the canopy and contextual behaviour. The primary result from Thorpe and Crompton's (2005) study was that support diameter, taken as an indicator of support compliance (i.e. the smaller the support, the more flexible it is), followed by support type and support number, had the biggest influence on locomotor repertoire of orangutans and influenced the ways in which they progressed through the complex, arboreal habitat. This was followed up by a detailed classification system solely for orangutans, using Hunt et al's (1996) standard system as a framework (Thorpe and Crompton, 2006). Further research has stemmed from this, investigating, in detail, aspects of orangutan locomotion and their interaction with flexible (compliant) arboreal supports (Thorpe et al., 2007a, b, 2009). It is this interaction between orangutans and support compliance that is of particular interest as they are the largest, predominantly arboreal mammal to cope with this complex habitat in order to find food, mates and avoid predators, such as the Sumatran tiger; *Panthera tigris sumatrae* (Cant, 1992). Furthermore, they are the only large-bodied hominoid remaining predominantly in the ancestral habitat, and therefore, the likelihood of orangutan evolving specific specialisations to this complex habitat are high (e.g. Thorpe et al., 2009).

1.3.3 Positional behaviour and the use of compliant arboreal supports

The importance of support compliance (flexibility) and its impact on the behaviour of arboreal primates was first highlighted by Grand (1972). Grand (1972) observed two primates of similar body mass (gibbons and macaques) and noted their different postural strategies when feeding on the smallest, and thus most flexible, branches in the terminal branch niche (TBN; the branches at the edges of the tree crown). The macaques remained above the support, whereas the gibbons suspended below it. By being in suspension below the support, the gibbons dampened the oscillations of the compliant support and maintained a more stable position compared to the macaque (Grand, 1972). Since then, many more studies, both in the field and the laboratory, have incorporated the compliant properties of the supports as an important variable that is likely to impact on the positional behaviour of arboreal species (e.g. Cant, 1992, 1994; Schmitt, 1999, 2003; Thorpe and Crompton, 2005, 2006; Thorpe et al., 2007a, b, 2009; Young, 2009).

Cant (1994) summarised the ways in which support compliance would be expected to impact on primates of different body mass and morphology during travel. Smaller primates were predicted to ignore compliance, as even small supports would be relatively stiff beneath their body mass, whereas medium-sized primates (e.g. long-tailed macaques, adult male body mass: 5.5 kg; Cant, 1988) were proposed to adjust for compliance e.g. waiting for a support to stop oscillating after landing at the end of a leap before continuing. In terms of energetics this actually results in a loss of energy because when the monkey lands on the branch it loses potential energy that has to be regained via climbing (Alexander, 1991). Since then, studies have shown that medium-sized

arboreal primates also cope with support compliance through the use of compliant quadrupedal gaits (where the limbs are tightly flexed) and diagonal sequence, ambling gaits (see Schmitt, 1999, 2003; Larney and Larson, 2004; Lemelin et al., 2003; Young, 2009). This lowers their centre of gravity which improves their balance on small supports (Schmitt, 1999, 2003) and enables them to maintain a least one limb in contact with the support at all times, resulting in a flatter centre of mass trajectory, which helps to reduce oscillations of the support (e.g. Larney and Larson, 2004).

In theory, however, if the natural frequency of a support is high enough (or the locomotion of the animal slow enough) any stored elastic energy in the support can be used be the animal (Alexander, 1991), although Alexander (1991) also refers to unlikelihood of this in most primates due to their small size. Demes and colleagues (1995) undertook a study investigating the possibility of energy return from a vertical compliant support during leaping in vertical clingers and leapers e.g. *Indri indri* (mass 7-8 kg). However, no energy return from the support was considered to occur as the animals took off from the support before the point of elastic return, and thus a loss of energy to the support was more likely (Demes et al., 1995). The possible use of branch compliance to aid locomotion has also been observed in other medium-sized primates when leaping and Hunt et al (1996) defined a mode called 'pumping leap', whereby a horizontal support is oscillated a number of times beneath the animal via forceful extension of the limbs before taking off to cross a gap. This behaviour has been observed in long-tailed macaques (*Macaca fascicularis*) on Sumatra (Myatt, pers. obs) and black howler monkeys (*Alouatta*

caraya) in Brazil (Thorpe, pers. obs), and although no further detail regarding the timing of take-off, and the possible use of energy is known, this method does appear to add distance to the leap (Hunt et al., 1996).

Although, these small and medium-sized primates were not predicted to be able to use support compliance, Cant (1994) had predicted that large-bodied primates, such as the great apes, would be able to utilise the compliance of a support during locomotion. Observations of Chevalier-Skolnikoff and colleagues (1982) were the first to note that orangutans employ a form of gap crossing where they oscillate a flexible support back and forth until the amplitude of the oscillations is great enough to enable them to cross the gap. This method, termed 'tree sway' has since been discussed or observed in a number of studies (Sugardjito and van Hooff, 1986; Cant, 1992, 1994; Povinelli and Cant, 1995; Thorpe and Crompton, 2005, 2006; Thorpe et al., 2007a, 2009). Thorpe and Crompton (2006) provided a wider definition for this locomotor mode, termed simply 'sway' which encompasses both the use of small trees as the vehicle support (that used to cross the gap) and the use of vertically hanging lianas to achieve the same result (see Fig. 1.7), together with a separate mode 'ride' which refers to the oscillation of a support in one direction only.

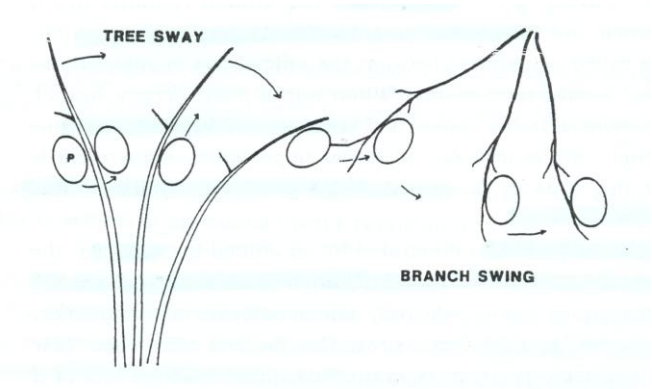

Fig. 1.7. Forms of sway used by orangutans, using either small trees or lianas (taken from Cant, 1994).

Although, from the earlier studies (e.g. Chevalier-Skolnikoff, 1982; Sugardjito and van Hooff, 1986; Cant, 1992, 1994; Povinelli and Cant, 1995; Thorpe and Crompton, 2005, 2006) the ability of orangutans to utilise compliance was apparent, it wasn't until a study by Thorpe et al (2007a) that the energy-saving role of sway became evident. From calculations of the mechanical work required to cross a gap using tree sway, in comparison to the mechanical work used to jump the same gap, or climb down and cross it terrestrially, Thorpe et al (2007a) found that sway was, in fact, the least costly option of the three for this large-bodied ape and may, therefore, be the most economical way for orangutans to move through the canopy (Thorpe et al., 2007a). To date, the use of tree sway has not been studied in detail in the other non-human apes and although its presence within the locomotor repertoire of gorillas and chimpanzees has been referred to, it does not appear to occur often (Doran, 1993a, b; 1996; Remis, 1995) and details of its form (i.e. sway or ride) are not yet known. Sway, therefore, appears to play a particular role in orangutan

locomotion, in comparison to the other apes, most likely due to their predominantly arboreal lifestyle in combination with their large body mass (Thorpe et al., 2007a).

Additional details of sway in orangutans, however, are not yet known, such as the different postures used during the movement of the support (Thorpe and Crompton, 2005, 2006), and how these may be related to the gap crossing context or age-sex class, is not yet understood. This is partly due to the difficulty in recording these complex behaviours using the standardised classification systems, as numerous body positions can be maintained during a single sway or ride movement (Thorpe and Crompton, 2005, 2006). Therefore, new methods of recording need to be developed before we can expand our understanding of these interesting behaviours that appear to play an important role in enabling orangutans to navigate their complex arboreal habitat effectively.

Support compliance, however, is not always beneficial. As body mass increases, the likelihood of supports bending and breaking beneath their body mass also increases, as does the risk of falling (Cartmill, 1985; Povinelli and Cant, 1995). Furthermore, the ability to maintain balance on top of supports, as either the supports get smaller, or body mass increases, becomes more difficult as they are unable to maintain the large contact torques required to balance (Grand, 1972; Cant, 1992, 1994; Povinelli and Cant, 1995). Therefore, while smaller primates are able to use above support postures behaviours more easily e.g. (Grand, 1972; Dunbar and Badam, 2000; Prates and Bicca-Marques, 2008), the non-human great apes are expected to use more suspensory postures.

Adaptations to suspensory behaviours are reflected in the morphology of all the apes, including features such as the ability to completely abduct the humerus and a wider range of scapular motion (see Hunt, 1991, 1996; Pilbeam, 1996) and suspensory behaviours form part of the repertoire of all the non-human apes (e.g. Hunt, 1992a, b; Doran, 1993, a, b; Remis, 1995; Fleagle, 1999; Thorpe and Crompton, 2005, 2006).

Recent studies, however, have shown that it is the use of orthograde postures in general, both suspensory and compressive, that characterise the positional behaviour of the non-human apes (Thorpe and Crompton, 2006; Crompton, et al., 2008) and enable them to use the most compliant supports. Orangutans, in particular, are expected to have developed specific abilities to cope with support compliance as they are the only large-bodied hominoid to remain in an arboreal habitat. Studies of orangutans, have identified specific locomotor behaviours including the compressive hand-assisted bipedalism (Thorpe et al., 2007b) and the suspensory, pronograde suspension (Thorpe et al., 2009) that enable their use of the most compliant supports. By enabling progression on the smallest supports these behaviours provide better access to food at the edges of trees in the TBN and place the orangutans closer to the edges of the gaps that need crossing (Thorpe et al., 2007b, Thorpe et al., 2009).

Orangutan gait, in general, is characteristically slow and un-patterned, using a combination of both compressive and suspensory behaviours which helps to reduce the oscillations of the supports (Thorpe and Crompton, 2005, 2006; Thorpe et al., 2009). During hand-assisted bipedal

locomotion, one of the modes enabling use of compliant supports, the majority of body weight is borne by the hindlimbs, but the forelimbs assist with balance or bear some, but not the majority of body weight, often in suspension above the head (Thorpe and Crompton, 2005, 2006; Thorpe et al., 2007b). This enables progression on the smallest supports by lowering the body's centre of mass closer to the support (due to shorter legs), whilst keeping the long forelimbs free to assist with balance and reach for food (Thorpe et al., 2007b). Such behaviours have also been observed in the other non-human apes, although in chimpanzees hand-assisted bipedal postures were actually used on larger, rather than the more compliant supports (Hunt, 1996; Stanford, 2004, 2006).

Pronograde suspension, on the other hand, is a behaviour unique to orangutans and thought to have evolved since their split from the last common ape ancestor (Thorpe et al., 2009). Pronograde suspension is thought to enable progression on the smallest supports because it involves suspension from multiple limbs beneath a support, with the torso in a pronograde (horizontal) orientation (Hunt et al. 1996; Thorpe and Crompton, 2006; Thorpe et al., 2009). Both of these modes are similar in that they utilise multiple supports, both to bear weight and for balance. Multiple support use enables orangutans to distribute their mass more evenly, and also provides security should one support break. Furthermore, they are able to move and test the next support with one limb, without letting go of the previous support, thus reducing the risks of moving amongst the most compliant supports (Thorpe and Crompton, 2005, 2006; Thorpe et al,

2007a, b, 2009). Therefore, it would appear that the use of multiple supports plays a fundamental role in the success of orangutans in their arboreal habitat.

The use of multiple supports may also be important during the maintenance of postural behaviours in orangutans. However, postural behaviours and their relation to the habitat are less well quantified than locomotion. As feeding is one of the key behaviours for any primate, and the majority of the most nutritionally beneficial food is located on the smallest supports in the TBN (Grand, 1972; Houle et al., 2007), we would expect to see specific postural strategies for feeding in this niche, particularly in the large-bodied hominoids. Previous studies have predicted an increased use of suspension during feeding in the large-bodied hominoids, in line with the theories regarding the difficulty of animals of increasing mass maintaining balance on top of small supports (Grand, 1972; Cant, 1992, 1994; Povinelli and Cant, 1995). Such a relationship between feeding and suspensory behaviours has been observed in the non-human apes, for example, unimanual arm-hanging formed 95.7% of the feeding observations in chimpanzees (Hunt, 1992a), and gibbons and orangutans predominantly use suspensory postures when feeding and travelling (Cant, 1987a, b; Fleagle, 1999; Thorpe and Crompton, 2005, 2006, 2009; Thorpe et al., 2009). However, it has also been predicted that above a certain threshold, an increase in body mass will result in an inability to use the most compliant supports, and the largest arboreal primates will use stiffer supports and less suspension (Grand, 1972; 1984; Ripley, 1979). In general, evidence from field studies, for both an increased use of suspension in primates of larger body mass, and the existence of a body mass threshold, is limited. Gibbons were found to use

suspension less than their heavier relatives, the siamangs (Harvey et al., 1986), but a comparison of gibbons and chimpanzees did not support the theory, as gibbons were more suspensory than chimpanzees (Hunt, 1991).

While there is some evidence that the heaviest of the predominantly arboreal apes, flanged adult male orangutans, use stiffer supports and less suspension than the other age-sex classes in some situations e.g. feeding on figs (see Cant, 1987a, 1992; Thorpe and Crompton, 2009), when feeding on other food types the distinction is not as clear (Thorpe and Crompton, 2009). To date, there has been no detailed study analysing the relationship between posture, support compliance, body mass and other ecological and habitat variables during feeding in orangutans, thus such a study may reveal further specialisation in orangutans. As adaptations for locomotion on small supports involve the use of multiple supports (Thorpe and Crompton, 2005, 2006; Thorpe et al., 2007a, b, 2009), one would also expect this to play a role during feeding. When using multiple supports a slight change in emphasis from balance to weight-bearing and subtle adjustments in the positioning of the different limbs is likely to enable orangutans to control the effects of support compliance and maintain stability (see Thorpe et al., 2009).

One of the reasons this variation and detail has yet to be studied is due to the difficulties in collecting such data from the field. While traditional classification systems provide a valuable overview of the positional behaviour repertoire of a species in the wild (e.g. Hunt et al., 1996; Thorpe and Crompton, 2006) they do not enable the recording of multi-limb, multiple support

behaviours in detail. Rather, only the main weight-bearing limb positions are taken into account and behaviours grouped into overall modes and sub-modes (Hunt et al., 1996; Thorpe and Crompton, 2006). Thus there is scope for a method to enable the finer details and spatial arrangement of limbs and support use during positional behaviours to be developed, that can also be quantitatively analysed, to shed light on the specific ways in which large-bodied hominoids, such as orangutans, are adapted to feed and move in their complex arboreal habitat.

Such a method might be adapted from methods used to record human movement in real-time, such systems, grouped under the title, movement notation, have long been used to record various styles of dance, including ballet, tap, folk and ethnic dance (Eshkol and Wachman, 1958; Knust, 1959; Scripps, 1965; Causley, 1967; Sutton, 1981; Hutchinson, 1990, 1996). Other aspects of human positional behavior, such as sitting (Kember, 1976) have also been recorded. Notation systems therefore appear capable of accurate recreation of complex behaviors from large scale (whole body) positioning through to detailed facial expressions (Knust, 1959; Causley, 1967; Sutton, 1981; Hutchinson, 1990, 1996; Eshkol and Wachman, 1958; Scripps, 1965) and may provide a base on which to build a system for primates. Commonly used methods of movement notation include Labanotation (Hutchinson, 1996); Eshkol-Wachman Movement Notation (Eshkol & Wachman, 1958), Benesh Movement Notation (Causley, 1967) and Sutton Movement Writing (Sutton, 1981).

A number of these techniques have been utilized in animal studies, particularly in the field of motor control (Eaton, 1992; Iwaniuk and Whishaw, 1999; Foroud et al., 2004; Vasey et al., 2006). However, to date, data from animal studies have either been captured on video and transcribed using notation later (Foroud et al., 2004; Vasey et al., 2006), or recorded live using multiple observers for different body segments (Carlson et al., 2000; Carlson pers. comm.). These techniques are not practical for most primate field studies, which often involve many hours of observation every day, over long periods. This may be one of the reasons that the use of movement notation has, to date, generally been neglected by primate field researchers in favor of the pre-determined definitional classification systems. However, it may be possible to simplify or adapt some of these methods to provide an additional method by which to record primate positional behaviour in the field, without the use of video cameras, which are often impractical due to factors such as battery life and speed of set up. Therefore, the next stage in the study of orangutan positional behavior appears to be a detailed exploration of multiple support use during key locomotor and postural behaviours, to provide a deeper insight into the ways in which these animals cope in their complex, flexible habitat. By developing a finer understanding of the dynamics between orangutans and their compliant environment, we can relate this to differences observed in morphology, thus building on our understanding of the form-function relationship in the hominoids and the evolution of specialisations and locomotor diversity in this group.

1.4 Thesis objectives and structure

The objective of this thesis is to expand our understanding of the morphology of the great apes, in addition to obtaining a greater knowledge of the relationship between positional behaviour and habitat use in the most specialised of the great apes (the orangutan) in order to provide greater insight into the influences and constraints acting upon them and to provide understanding of the evolution of diversity within the hominoids. Orangutans were selected as the focal species for the field study because they are the largest, predominantly arboreal ape, and there is already some evidence that they have evolved specialist locomotor behaviours e.g. pronograde suspension, not used by the other non-human apes. Therefore, more subtle variations and adaptations to the various challenges of the complex arboreal habitat may be present in this species. A key part of this thesis is to introduce new methods of both data collection and analysis by which we can gain a more detailed insight into aspects of form and function in the non-human apes. By providing more specific information on these relationships, this thesis aims to develop a greater understanding of the morphology-behaviour-habitat interface in our closest living relatives, the non-human apes.

Specifically the thesis will address the following questions:

1. Are there variations in the macro-architecture in the fore and hindlimbs of the non-human apes that reflect the different frequencies with which they use different positional behaviours or differences in habitat use? Are there alternative methods to geometric scaling by which we can compare individuals of different body mass?

2. Do muscle fibre type proportions in key locomotor muscles differ between non-human ape species that differ in their predominant behaviours and habitat use, reflecting morphological adaptations on a finer scale within the hominoids?

3. What is the postural variation used during oscillatory behaviours in orangutans and how can this be classified?

4. Do orangutans have specific postural adaptations for coping with support compliance when feeding in the terminal branch niche? How do other ecological and behavioural factors e.g. age-sex class, feeding method, interact with support stiffness during feeding?

To answer these questions the thesis will be structured as follows: Chapters 2 and 3 will present muscle architecture data from the hind and forelimbs of the non-human apes, and provide alternative methods by which to undertake species comparisons. Chapter 4 will provide a comparison between chimpanzees and orangutans in the distribution of muscle fibre types through their triceps surae, a key locomotor muscle, to see if there are specialisations to their different behaviours and habitat use at the micro-architecture level. Chapter 5 will introduce a new method by which to record complex positional behaviour in primates, and chapter 6 will employ this method to record the postural variation in sway, as used by wild orangutans, and assess the use of a quantitative method to classify positional behaviour. The relationship between postural behaviours in orangutans and feeding in the terminal branch niche in relation to support compliance will be the focus of chapter 7. Finally chapter 8 will bring all the aspects of

morphology, behaviour and habitat together to discuss the implications of these results for the evolution of positional behaviour diversity in the non-human apes.

CHAPTER 2

HINDLIMB MUSCLE ARCHITECTURE IN NON-HUMAN GREAT APES AND A COMPARISON OF METHODS FOR ANALYSING INTER-SPECIES VARIATION.

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By relating an animal's morphology to its functional role and the behaviours it performs, we can further develop our knowledge of the causes and constraints of great-ape adaptations and the evolution of locomotor diversity in the hominoids. The comparison of muscle architecture between the different species of ape is often difficult because only small sample sizes are available. Further, samples are often comprised of different age-sex classes, so that many studies have had to rely on scaling techniques to remove body mass differences. The reliability of scaling techniques has however been questioned. As datasets increase in size, more reliable statistical analysis may be possible. Here we employ geometric and allometric scaling techniques and general linear models to establish the most appropriate method for comparing functional morphology in the non-human great apes. The results obtained highlight the importance of regressing data against a suitable body size variable to ascertain the relationship form (geometric or allometric) and choosing appropriate exponents by which to scale data, as large variations in outcome can occur. However, the use of GLMs appears to be a more promising method for the comparison of anatomical data, but larger sample sizes are needed to confirm this. Overall, the results obtained from the different methods showed little significant variation in muscle belly mass, fascicle length or physiological cross sectional area between the different species. This may reflect relatively close evolutionary relationships of the non-human great apes and/or a universal influence on morphology of generalised orthograde locomotor behaviours.

JPM conducted the data collection; analysed the data and wrote the manuscript. RHC assisted with data collection and aided in the writing of the manuscript. SKST assisted with data collection, discussion of the statistical analysis and aided in the writing of the manuscript.

2.1 Introduction

Studying the relationship between the functional anatomy of an animal, the behaviours it performs and the habitat it uses is crucial to any investigation of how the environment influences functional morphology, or conversely, how an animal's functional design impacts on its habitat use (Wainwright, 1991). Thus, by relating the functional anatomy of extant non-human great apes to the locomotor behaviours they perform in their different habitats, we can expand our knowledge of the influences and constraints upon great-ape adaptations and locomotor diversification in the hominoids (see Bock and von Wahlert, 1998; Payne et al., 2006; Vereecke, 2006).

The measurement of basic anatomical parameters including muscle belly mass and muscle fascicle length, enables factors such as muscle physiological cross-sectional area (PCSA) to be estimated and the core function of a muscle determined (e.g. Thorpe et al., 1999; Carlson, 2006; Payne et al., 2006). Fascicle length reflects the number of sarcomeres in series and the longer the fascicle length, the greater the maximum shortening velocity of the muscle fascicles (see Wickiewicz et al., 1984; Thorpe et al., 1999). PCSA, on the other hand, reflects the number of sarcomeres in parallel, and provides an indication of the maximum force a muscle can produce, when multiplied by the maximum isometric stress of vertebrate muscle (0.3 MPa; Wells, 1965). Therefore, a larger PCSA indicates an ability to produce larger forces (Sacks and Roy, 1982; Zajac, 1992; e.g. Thorpe et al., 1999; Carlson, 2006; Payne et al., 2006, Channon et al., 2009; Michilsens et al., 2009).

In recent years, the number of studies recording these features of hindlimb muscle architecture in non-human apes has increased (e.g. chimpanzee: Thorpe et al., 1999; Carlson, 2006; gibbon and siamang: Vereecke, 2006; Channon et al., 2009; all apes: Payne et al., 2006). However, due to the poor availability of non-human ape cadavers, sample sizes are often very small; consist of varying age-sex classes, and can take many years to collate, all of which complicates inter-specific comparisons of functional ability. Furthermore, non-human apes range in size from approximately 5 kg in gibbons (Vereecke, 2006; Channon et al., 2009) to over 200 kg in gorillas (Zihlman and McFarland, 2000). Such wide variation in body mass needs to be taken into consideration if we are to be able to interpret inter-specific differences in morphology and the implications of such differences for the dynamic between animals and their habitat.

The calculation of a per-body mass ratio, where the variable of interest is divided by a measure of body size, such as body mass, may appear to be an appropriate way to remove differences due to body size (Packard and Boardman, 1987; Nevill et al., 1992). However, this is only suitable in instances where the physiological variable varies isometrically with body size (Tanner, 1949; Cochran, 1957; Schmidt-Nielsen, 1984; Packard and Boardman, 1987; Nevill et al., 1992). Two animals are considered isometrically (or geometrically) similar if one could be made identical to the other by multiplying all length dimensions by the same factor (Alexander, 2000). In such cases, plotting the variable of interest (e.g. muscle PCSA), against a measure of body size (e.g. body mass) would result in straight line passing through the origin (see Schmidt-Nielsen, 1984; Packard and Boardman, 1987). Where anatomical data does scale geometrically, masses are proportional to $(\text{mass})^{1}$, lengths to $(\text{mass})^{1/3}$ and areas to

$(mass)^{2/3}$ (Alexander et al., 1981; Alexander, 2003). This relationship has been used in numerous previous studies of ape anatomy to normalise data and remove the effects of body mass from the analysis (Thorpe et al., 1999; Payne et al., 2006; Oishi et al., 2008, 2009; Channon et al., 2009; Michilsens et al., 2009). The method may be justified for intra-specific comparisons (as in Thorpe et al. 1999), because animals of the same species are more likely to be geometrically similar (although ontogenetic changes should also be taken into account). However, it has been argued that geometric normalization is unlikely to be appropriate for inter-specific comparisons because true geometric scaling rarely occurs in nature due to variations during ontogeny or evolution, and adaptations to different lifestyles (Alexander et al., 1981; Nevill et al, 2005). Therefore, the use of geometric scaling to assess species differences accurately may not always be appropriate. Regression analysis should be performed prior to normalisation to see if data plot as a straight line through the origin, even for intra-specific comparisons (see Tanner et al., 1949; Alexander et al., 1981; Packard and Boardman, 1987, 1999; Nevill et al., 2005).

More commonly, a plot of the variable of interest against the measure of body size generally results in a linear relationship that does not pass through the origin, or a curvilinear relationship, and the relationship is described as allometric, whereby the variable does not alter in direct proportion to body size (see Smith, 1984; Packard and Boardman, 1987; Brown et al., 2000; Biewener, 2003).The use of power function models, or allometric equations, to scale physiological variables is well established (e.g. Kleiber, 1950; Alexander et al., 1981; Schmitt-Nielsen, 1984; Pollock and Shadwick, 1994; Nevill and Holder, 1995; Brown et al., 2000) and takes the form,

Equation 2.1 $Y = aX^b$

where *a* and *b* are constants and X is body mass. These can be converted into a linear relationship by regressing logarithms of the data to give the equation:

Equation 2.2 $\log Y = \log a + b \log X$

The slope of the line, *b*, is the exponent of the power function and can be expressed as either a decimal or fraction (Schmidt-Nielsen, 1984; Alexander, 2000). Allometric equations have been established for many biological variables such as rate of oxygen consumption and metabolism (see Schmidt-Nielsen, 1984 for examples). However, rather than scaling as third powers as predicted by isometry, such variables often scale as quarter powers of body mass (M) e.g. mammalian metabolic rate has been found to scale to $M^{3/4}$ and lifespan to $M^{1/4}$ (Schmidt-Nielsen, 1984; Brown et al., 2000). Not all studies, however, agree on the values of such exponents. Variations have been identified depending on the range of body sizes studied and the conditions under which measurements are taken, particularly for metabolic scaling exponents (e.g. White and Seymour, 2005; White et al., 2007; White et al., 2009; Isaac and Carbone, 2010; Vaca and White, 2010). Furthermore, even if there is agreement over the exponents established, the use of ratios to normalise the data may still introduce bias into the data (Packard and Boardman, 1999). Nevertheless, the use of allometry for scaling anatomical data has remained a key method to compare data between animals of different body mass (e.g. Pollock and Shadwick, 1994; Eng et al., 2008; McGowen et al., 2008).

An alternative approach has also been suggested to enable comparison of morphological or physiological data, which is based on statistical models that take account of body size

variation, but remove the need for scaling. These include Analysis of Covariance (ANCOVA) on regression data and General Linear Models (GLMs) with body mass as a covariate (e.g. Packard and Boardman, 1987, 1999; Green et al., 2005; Halsey et al., 2007; Portugal et al., 2009). Rather than trying to remove the effects of body mass through the use of ratios, these models analyse the amount of variation in the variable of interest due to both body mass and other aspects of interest e.g. species differences (Packard and Boardman, 1987; 1999; Portugal et al., 2009). They may thus provide a more robust analysis of morphological data where there are differences in body mass between subjects. The dual aims of the current study, therefore, were to add to the increasing dataset on non-human ape muscle architecture, and to explore the use of different methods to compare such data.

2.2 Materials and methods

The new material used in this study comprised one chimpanzee (*Pan troglodytes;* PtsmL and R), one bonobo (*Pan paniscus;* Ppam), two gorilla (*Gorilla gorilla gorilla*; Gam, Gsm) and one orangutan (*Pongo abelii*; Oaf) cadavers that were fresh-frozen (see Table 2.1 for subject information). Data from the distal leg muscles of the right-hand side of Ptsm were not available but the proximal right leg muscles (PtsmR) were used in the analysis, as the opportunity to dissect both sides of one individual for comparison is rare due to the demands of collecting other data.

Table 2.1. Subject Information

Subject code	**PtsmL**	**PtsmR**	**Ppam**	**Gam**	**Gsm**	**Oaf**
Species	*P. troglodytes*		*P. paniscus*	*G. gorilla gorilla*	*G. gorilla gorilla*	*P. abelii*
Obtained from	Zoological Society London		Apenheul Zoo	Twycross Zoo	Twycross Zoo	Paington Zoo
Sex	M[1]		M	M	M	F
Body mass (kg)	50.20		41.92	175.00	152.00	54.00
Age at death (years)	ca. 11 (sub-adult)		ca. 22 (adult)	ca. 30 (adult)	ca. 18 (sub-adult)	ca. 45 (adult)
Cause of death	Group violence		Euthanasia	Fibrosing cardiomyopathy	Brain haemorrhage	Euthanised
Hindlimb dissected	Left and right[2]		Left	Left	Right	Right

[1]M: male, F: female

[2]Limbs on both the left and right side were available for dissection from this individual and therefore two different subject codes are given to distinguish between them.

2.1.1 Anatomical measurements and functional groupings

Muscle fascia were removed, and muscles separated and identified before being removed systematically, with their complete tendons attached. Points of origin and insertion were recorded. Muscle-tendon unit lengths were measured, including separate measurements for external tendon lengths at the origin and insertion, and muscle belly length. External tendon length was measured as the distance from the either the most proximal (tendon of origin) or distal (tendon of insertion) muscle fibres to the point of tendon attachment to the bone. Any external tendon was then removed and muscle belly mass (including internal tendons)

recorded. Finally, the muscle belly was cut, either along the line of the internal tendon (pennate muscles), or along the centre of the belly (parallel fibred muscles) to reveal the full length of the muscle fibres, and three measurements of muscle fascicle length were made at different locations throughout the belly. Muscle fascicle length is a measurement of the bundle of muscle fibres that is visible to the naked eye. Muscle mass was measured to the nearest 0.1 g, and tendon mass to the nearest 0.01 g. All lengths were measured to the nearest millimetre using a metal rule.

Physiological cross-sectional area (PCSA) was calculated using the equation:

Equation 2.3 $PCSA = m/\rho l$

where m is muscle belly mass in grams, ρ is the density of fresh muscle (1.06 g cm^{-3}, Mendez and Keys, 1960) and l is muscle fascicle length in cm. In primates the angle of the fascicles to the tendon (pennation angle) is generally less than 30^{o} in fore- and hind-limb muscles (Thorpe et al., 1999), thus $\cos\theta$, normally present in this equation ($PCSA = (\cos\theta \times m)/\rho l$)) is approximately one and can be omitted.

To enable comparison, muscles were grouped according to their primary function, based on previous studies of ape muscle anatomy (Swindler and Wood, 1973; Payne et al., 2006; see Table 2.2 for groupings). The intrinsic hip and foot muscles were not included in the main analysis as measurements were not recorded for all subjects. To increase the size of the data set to enable more robust comparison of scaling techniques, raw data from previous studies were obtained for analysis of the scaled data and for GLM analysis. Data for chimpanzees

were taken from Thorpe (1997) (chimp 93 and chimp 94) and Thorpe et al. (1999) (chimp 95) and data for one bonobo (Pp), two gorillas (Gm and Gj) and one orangutan (Ojm) were taken from Payne et al. (2006) (note that data for Gp and Ojf from their study were not included as they were incomplete datasets, and data from Oam were not used because this subject was fixed in alcohol).

Table 2.2. Functional muscle groups for the hindlimb

Muscle group	Muscles
Gluteals	Gluteus maxmimus, gluteus medius, gluteus minimus and scansorius
Adductors	Adductor magnus, adductor brevis, adductor longus and pectineus
Knee extensors	Rectus femoris and the vasti
Hamstrings	Biceps femoris (long and short heads), semimembranosus, semitendinosus
Knee and hip flexors	Gracilis and Sartorius
Knee flexors	Popliteus, gastrocnemius lateralis*, gastrocnemius medialis*
Plantarflexors	Gastrocnemius lateralis*, gastrocnemius medialis*, soleus, plantaris and tibialis posterior
Dorsiflexors	Tibialis anterior, extensor hallucis longus, extensor digitorum longus
Digital flexors	Flexor hallucis longus, flexor digitorum longus, flexor digitorum fibularis
Everters	Peroneus longus and peroneus brevis

*Gastrocnemius lateralis and medialis were included in both the knee flexors and the plantarflexors as they are biarticular muscles, with roles in both functions.

To obtain an overview of the maximum force generating capacity of each muscle group, muscle belly masses and PCSA values within a group were simply added together. However, muscle fascicle length was calculated as a weighted harmonic mean to take into account the different sizes of the muscle fibres in a group, using the equation:

Equation 2.4 $$L = \sum m_j / \sum (m_j / l_j)$$

Where L is the group fascicle length, for a group where the jth member has a mass m_j and a fascicle length of l_j (Alexander et al., 1981).

2.2.2 Scaling of data

Before scaling using any method, regression analyses should be performed to establish the relationship between the variable of interest and body mass to decide which method of scaling is appropriate. However this has rarely been performed in previous studies of muscle architecture (e.g. Thorpe et al., 1999; Carlson, 2006; Oishi et al., 2008, 2009; Channon et al., 2009; Michilsens et al., 2009). Thus, regressions of log-transformed data (to ensure linearity) of the three physiological variables of interest (belly mass, fascicle length and PCSA) from all studies were plotted against body mass (kg) (Minitab®, USA) and found to scale allometrically with body mass. Allometric scaling exponents were then established for muscle belly mass, fascicle length and PCSA for each functional muscle group, along with overall exponents and a mean exponent (calculated from the muscle group exponents). Raw data were then scaled using the individual group allometric exponents.

Although the use of geometric scaling was found to be inappropriate in this instance, for the purposes of this chapter we additionally applied geometric scaling (see Alexander, 1981) to explore how the conclusions of previous studies of ape muscle architecture that were obtained using geometric scaling (see Thorpe et al., 1999; Payne et al., 2006; Channon et al., 2009) compare to the alternative methods proposed herein.

2.2.3 Statistical analysis

General linear models (GLMs) on log-transformed data with body mass as a covariate were used to assess whether differences between individuals reflected species differences and/or

variation in body mass, based on the combined data set from all studies. GLMs were performed using Minitab® (USA) for each physiological variable, for each muscle group across the four species. To achieve a model of best fit the main effects 'species' and 'body mass' and the interaction 'species*body mass' were first included. Backward elimination was then used to remove each non-significant term (significance taken at the $p = 0.05$ level), one at a time, until the best fitting model remained (see Grafen and Hails, 2002). In cases where either the interaction or species were found to have a significant effect, Tukey's post-hoc tests were performed to establish which species were significantly different ($p = 0.05$).

2.3 Results

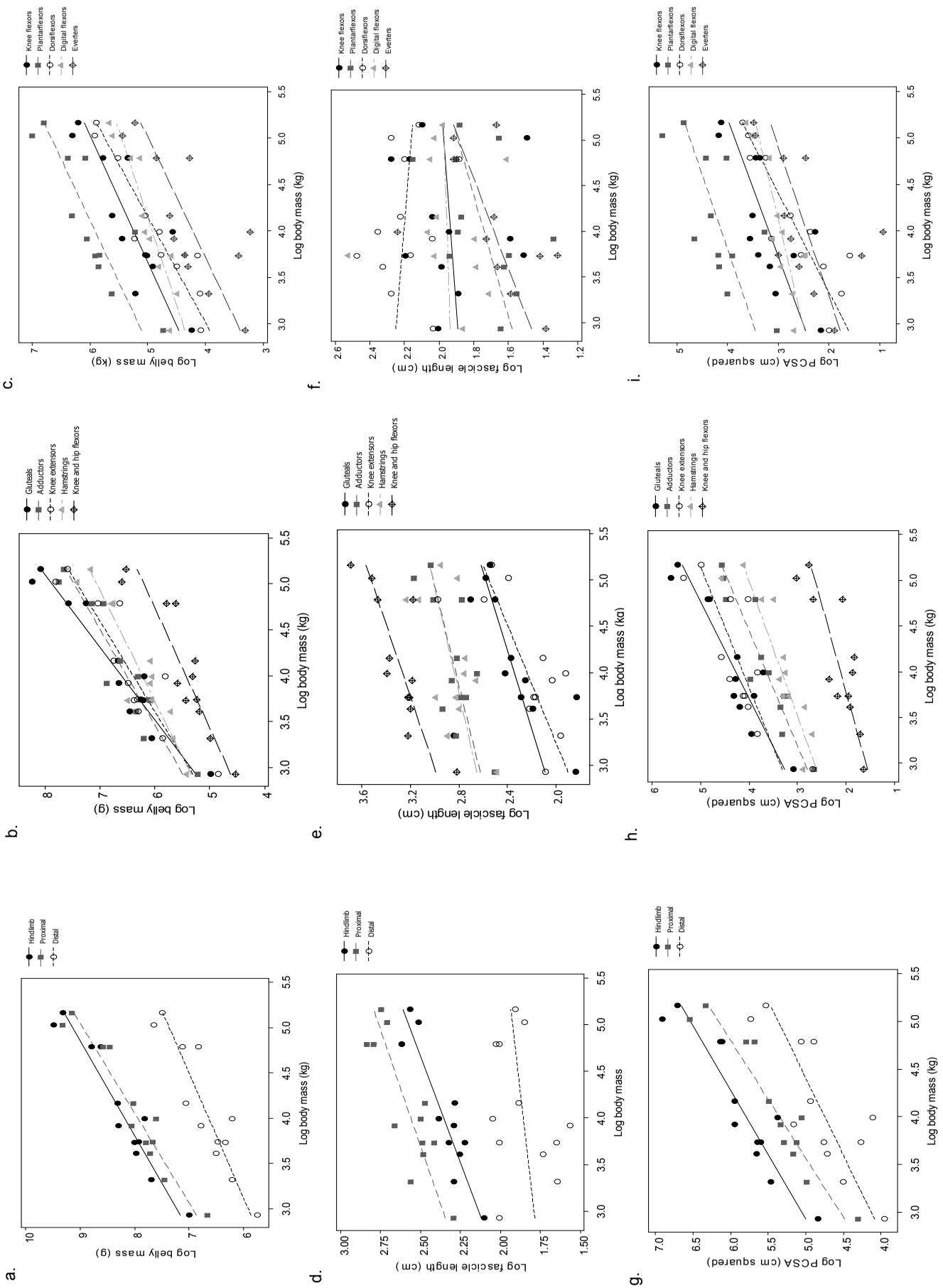
2.3.1 Descriptive Anatomy

Raw data for subjects PtsmL and R, Ppam, Gam, Gsm and Oaf are provided in appendix I. In general the hindlimb muscle anatomy in this study followed that observed in previous studies (e.g. Swindler and Wood, 1973; Thorpe et al., 1999; Payne et al., 2006) and origins and insertions were similar between all subjects. Variations observed included the absence of scansorius as a clearly separate muscle in all subjects except the adult female orangutan (Oaf), and the presence of a number of muscle belly divisions in different subjects. Adductor magnus was present as two bellies in the bonobo and Gam, and adductor brevis was present in two parts in Gsm. Similarly the bonobo and Oaf also had two parts to their tibialis anterior muscle, whereas the other subjects only had one. It was possible to separate semimembranosus into its two parts, proprius and accessories, only in the bonobo.

The plantaris muscle was present in both limbs of the chimpanzee (PtsmR and PtsmL) and the bonobo, but was not present in the gorillas or orangutans. The digital flexor muscles showed variations in terms of both their presence and their insertions. Most notable was the presence of an additional digital flexor muscle in Oaf, termed flexor digitorum fibularis (see Schwartz, 1988), in addition to flexor digitorum longus and flexor hallucis longus. The muscle belly labelled flexor digitorum fibularis inserted onto digits three and four, whereas flexor hallucis longus inserted onto digit one. As flexor digitorum longus inserted onto digits two, four and five, the presence of all three muscle bellies resulted in single tendons inserting on all digits except digit four which had two tendons of insertion. In all other subjects in this study, except Gsm, the muscles flexor digitorum longus and flexor hallucis longus inserted onto all five digits, although the belly which provided a specific tendon of insertion differed between individuals. Gsm was unusual in that both flexor digitorum longus and flexor hallucis longus only had one tendon of insertion each, both inserting onto digit one.

2.3.2 Scaled data

Regressions of log transformed data are presented in Figure 2.1 for all data combined from this and previous studies (Thorpe 1997; Thorpe et al., 1999; Payne et al., 2006). All data scaled allometrically rather than geometrically, as the log-transformed data formed a linear relationship that did not fall through the origin in all instances.


a.
b.
c.
d.
e.
f.
g.
h.
i.
Hindlimb
Proximal
Distal
Gluteals
Adductors
Knee extensors
Hamstrings
Knee and hip flexors
Knee flexors
Plantarflexors
Dorsiflexors
Digital flexors
Everters
Log body mass (kg)
Log belly mass (g)
Log belly mass (kg)
Log fascicle length (cm)
Log PCSA (cm squared)

Equation components established from the regression figures provided in Figure 2.1 are given in Tables 2.3, 2.4 and 2.5 for belly mass, fascicle length and PCSA respectively. Muscle belly mass had a significant relationship with body mass in all instances with an overall mean scaling exponent of $M^{0.85}$ (Table 2.3). This is negatively isometric (i.e. below the exponent $M^{1.0}$ which would be predicted by isometry). Fascicle length did not show a significant linear relationship with body mass in any distal muscle group or in the gluteals, but there was a significant linear relationship with all other proximal muscle groups. The overall mean scaling exponent for fascicle length was $M^{0.15}$, which is also below that predicted by isometry ($M^{0.33}$; see Table 2.4). PCSA showed a significant linear relationship with body mass in all functional groups, except the everters (Table 2.5). The overall mean scaling exponent for PCSA ($M^{0.70}$) is reasonably close to that predicted by isometry, although the relationship remains allometric as the line does not pass through the origin.

Table 2. 3. Allometric equation constants for hindlimb muscle belly mass (g)

Muscle group	**a (±SE)[1]**	**b (±SE)**	***R²***	***p***
Overall				
Total	0.52 (±0.53)	0.94 (±0.13)	0.83	<0.001
Proximal	3.90 (±0.39)	1.01 (±0.09)	0.92	<0.001
Distal	3.73 (±0.43)	0.73 (±0.10)	0.83	<0.001
Proximal				
Gluteals	1.54 (±0.48)	1.27 (±0.12)	0.92	<0.001
Adductors	2.69 (±0.48)	0.96 (±0.11)	0.87	<0.001
Knee extensors	2.32 (±0.64)	1.02 (±0.15)	0.82	<0.001
Hamstrings	2.92 (±0.41)	0.83 (±0.10)	0.87	<0.001
KH flexors[2]	2.38 (±0.45)	0.76 (±0.11)	0.83	<0.001
Distal				
Knee flexors	2.26 (±0.59)	0.75 (±0.14)	0.71	<0.001
Plantarflexors	2.90 (±0.61)	0.76 (±0.15)	0.72	<0.001
Dorsiflexors	1.36 (±0.43)	0.88 (±0.10)	0.88	<0.001
Digital flexors	2.80 (±0.36)	0.53 (±0.09)	0.79	<0.001
Everters	1.15 (±0.86)	0.77 (±0.21)	0.58	0.004
Mean exp		**0.85 (±0.06)**		

[1]Equation takes the form $y = aM^b$, where M is body mass (kg) and a and b are provided above.

[2]Knee and hip flexors.

Table 2.4. Allometric equation constants for hindlimb muscle fascicle length (cm)

Muscle group	a (±SE)[1]	b (±SE)	R^2	*p*
Overall				
Total	1.48 (±0.13)	0.22 (±0.03)	0.84	<0.001
Proximal	1.75 (±0.17)	0.20 (±0.04)	0.72	0.001
Distal	1.59 (±0.31)	0.07 (±0.07)	0.08	0.390
Proximal				
Gluteals	1.41 (±0.49)	0.24 (±0.12)	0.22	0.073
Adductors	2.08 (±0.23)	0.19 (±0.05)	0.54	0.007
Knee extensors	0.99 (±0.40)	0.31 (±0.10)	0.52	0.008
Hamstrings	2.15 (±0.30)	0.17 (±0.07)	0.36	0.039
KH flexors[2]	2.24 (±0.23)	0.26 (±0.06)	0.67	0.001
Distal				
Knee flexors	1.78 (±0.49)	0.04 (±0.12)	0.00	0.752
Plantarflexors	1.14 (±0.36)	0.15 (±0.09)	0.23	0.114
Dorsiflexors	2.38 (±0.29)	-0.04 (±0.07)	0.04	0.562
Digital flexors	1.89 (±0.43)	0.02 (±0.10)	0.00	0.875
Everters	0.88 (±0.41)	0.20 (±0.10)	0.29	0.071
Mean exp		**0.15 (±0.04)**		

[1]Equation takes the form $y = aM^b$, where M is body mass (kg) and a and b are provided above.

[2]Knee and hip flexors.

Table 2.5. Allometric equation constants for hindlimb muscle PCSA (cm^2)

Muscle group	a (±SE)[1]	b (±SE)	R^2	*p*
Overall				
Total	2.83 (±0.42)	0.74 (±0.10)	0.84	<0.001
Proximal	2.11 (±0.38)	0.81 (±0.90)	0.89	<0.001
Distal	2.27 (±0.60)	0.62 (±0.14)	0.65	0.002
Proximal				
Gluteals	0.35 (±0.65)	0.97 (±0.16)	0.79	<0.001
Adductors	0.49 (±0.39)	0.79 (±0.09)	0.88	<0.001
Knee extensors	1.09 (±0.72)	0.76 (±0.17)	0.66	0.001
Hamstrings	0.63 (±0.46)	0.68 (±0.11)	0.79	<0.001
KH flexors[2]	0.02 (±0.46)	0.52 (±0.11)	0.69	0.001
Distal				
Knee flexors	0.49 (±0.77)	0.68 (±0.19)	0.53	0.004
Plantarflexors	1.63 (±0.82)	0.62 (±0.20)	0.50	0.010
Dorsiflexors	-1.14 (±0.64)	0.94 (±0.15)	0.79	<0.001
Digital flexors	1.22 (±0.37)	0.43(±0.09)	0.70	0.001
Everters	-0.06 (±1.20)	0.62 (±0.29)	0.32	0.056
Mean exp		**0.70 (±0.05)**		

[1]Equation takes the form $y = aM^b$, where M is body mass (kg) and a and b are provided above.

[2]Knee and hip flexors.

Figure 2.2 is an example of the different results obtained for the dorsiflexor muscle group PCSA depending on the scaling exponent used to normalise the data. This group was selected as an example because, depending on the exponent selected, it scaled either below the exponent predicted by isometry (i.e. $M^{0.67}$ for PCSA, labelled negatively isometric) or above (positively isometric). From Figure 2.2 it can be seen that although the general pattern of variation remains similar, the magnitude of the differences between different individuals varies and overall PCSA differs substantially. When a negatively allometric exponent was used ($M^{0.62}$: total distal hindlimb exponent in the current study) the magnitude of differences between different individuals increased compared to geometrically scaled data ($M^{0.67}$). However, when a positively allometric exponent was used ($M^{0.92}$: dorsiflexor muscle group exponent in this study), the magnitude deceased and there was no difference in PSCA between some individuals where variations were previously identified. This discrepancy was also apparent in the other muscle groups, for all physiological variables.

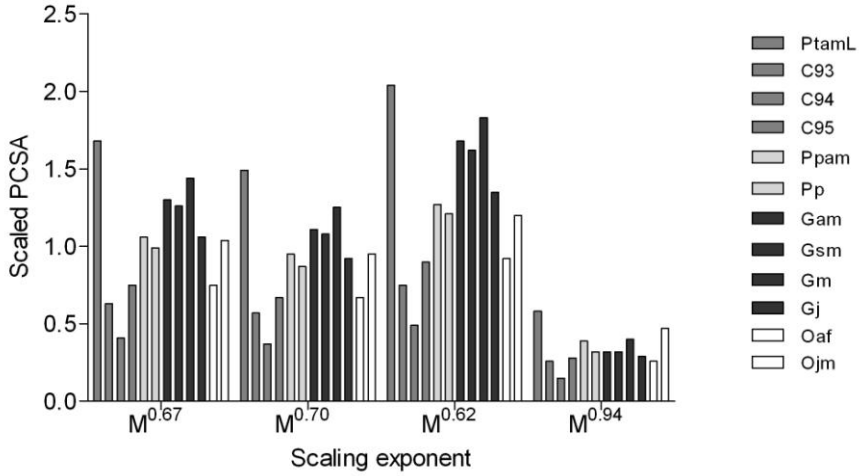


Fig. 2.2. Comparison of dorsiflexor PCSA scaled using the scaling exponents, $M^{0.67}$ (geometric exponent); $M^{0.70}$ (mean exponent); $M^{0.62}$ (distal hindlimb exponent); $M^{0.94}$ (dorsiflexor group exponent).

For overall comparison, muscle group data were scaled both geometrically and allometrically (using individual group exponents) and comparative data for fascicle length and PCSA are presented in Figures 2.3 and 2.4 respectively (belly mass data is not presented as the main interest in this study is the relationship between mobility and force production, rather than power output). There was a large amount of variation between individuals of the same species for all physiological variables, making it very difficult to visually compare the different species, in particular for PCSA (Figure 2.4). Observations of note include, firstly, the difference between the left and right proximal muscles of chimpanzee Ptsm, whereby the right limb had a larger PCSA than the left in the knee extensors (by 18.86 %) and hamstrings (47.14 %). In general, fascicle length was more uniform within the different species than was PCSA. The orangutans, however, differed greatly in both fascicle length and PCSA in the everters, with the adult orangutan (Oaf) having longer fascicles (by 47.5% based on allometric data) and a smaller PCSA (by 80.4 %) than the juvenile orangutan (Ojm). The juvenile orangutan also had a larger PCSA than did Oaf in a number of other groups including the hamstrings, knee and hip flexors, knee flexors, plantarflexors, dorsiflexors, digital flexors and everters. The two bonobos differed in PCSA, particularly in the digital flexors (Pp PCSA greater by 30.9%) and everters (Ppam PCSA greater by 31.5 %), and chimp 93 had a smaller PCSA than the other chimpanzees across all distal muscle groups. Within the gorillas, the gluteals, knee extensors, hamstrings and plantarflexors had a larger PCSA in Gsm than the other gorillas. Overall species differences were apparent in that the orangutans generally had smaller PCSAs, but the chimpanzees larger PCSAs in comparison to the other species. However, in the case of the digital flexors the orangutans appeared to have a greater PCSA than the other species.

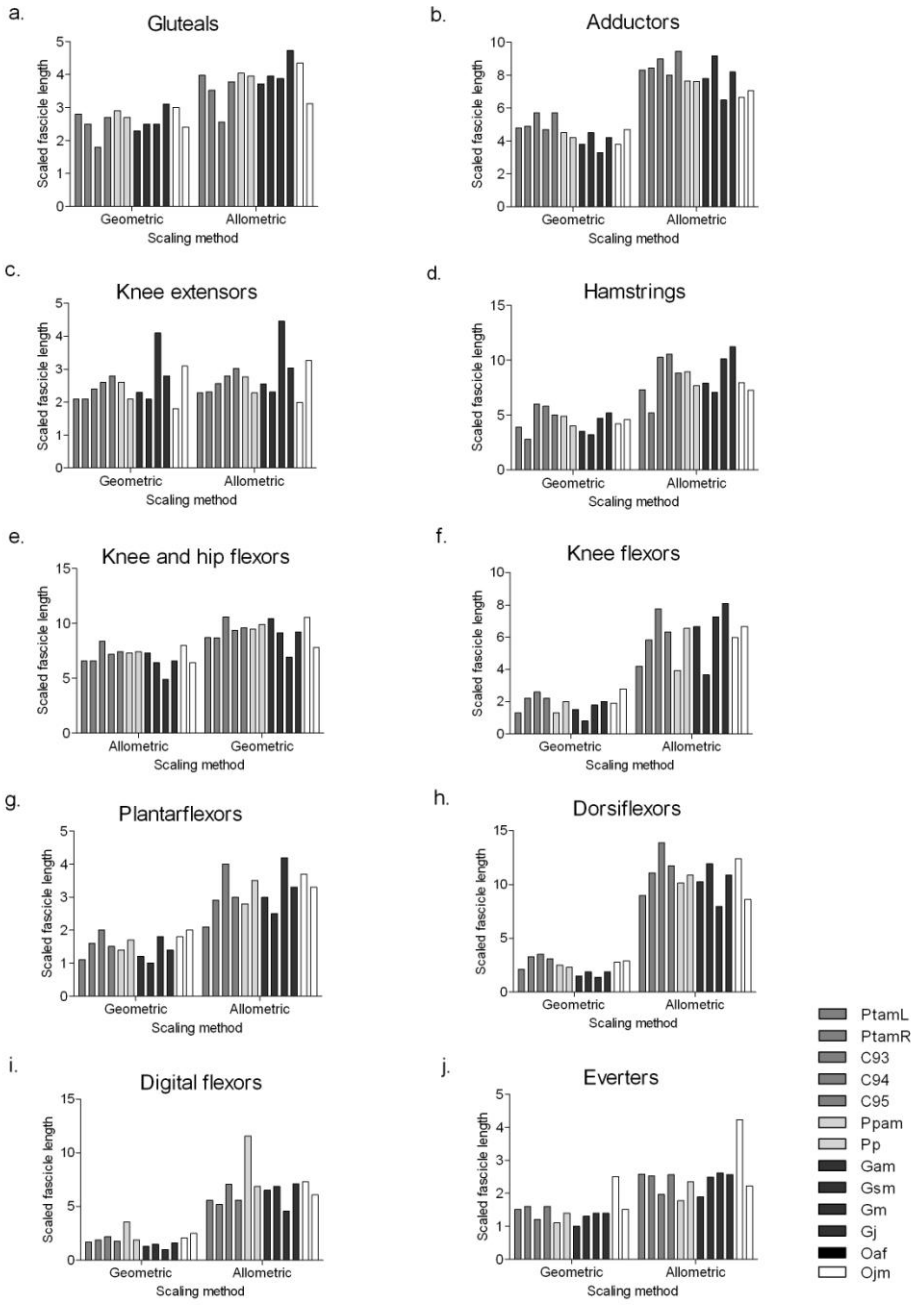


Fig. 2.3. Comparison of raw fascicle length data scaled using both geometric and individual group allometric exponents. a. gluteal muscle group $M^{0.24}$ (data for chimp 93 not available), b. adductors $M^{0.19}$, c. knee extensors $M^{0.31}$, d. hamstrings $M^{0.17}$, e. knee and hip flexors $M^{0.26}$, f. knee flexors $M^{0.04}$, g. plantarflexors $M^{0.15}$, h. dorsiflexors $M^{-0.04}$, i. digital flexors $M^{0.02}$, j. everters $M^{0.20}$. Figures f-j do not include data from PtsmR.

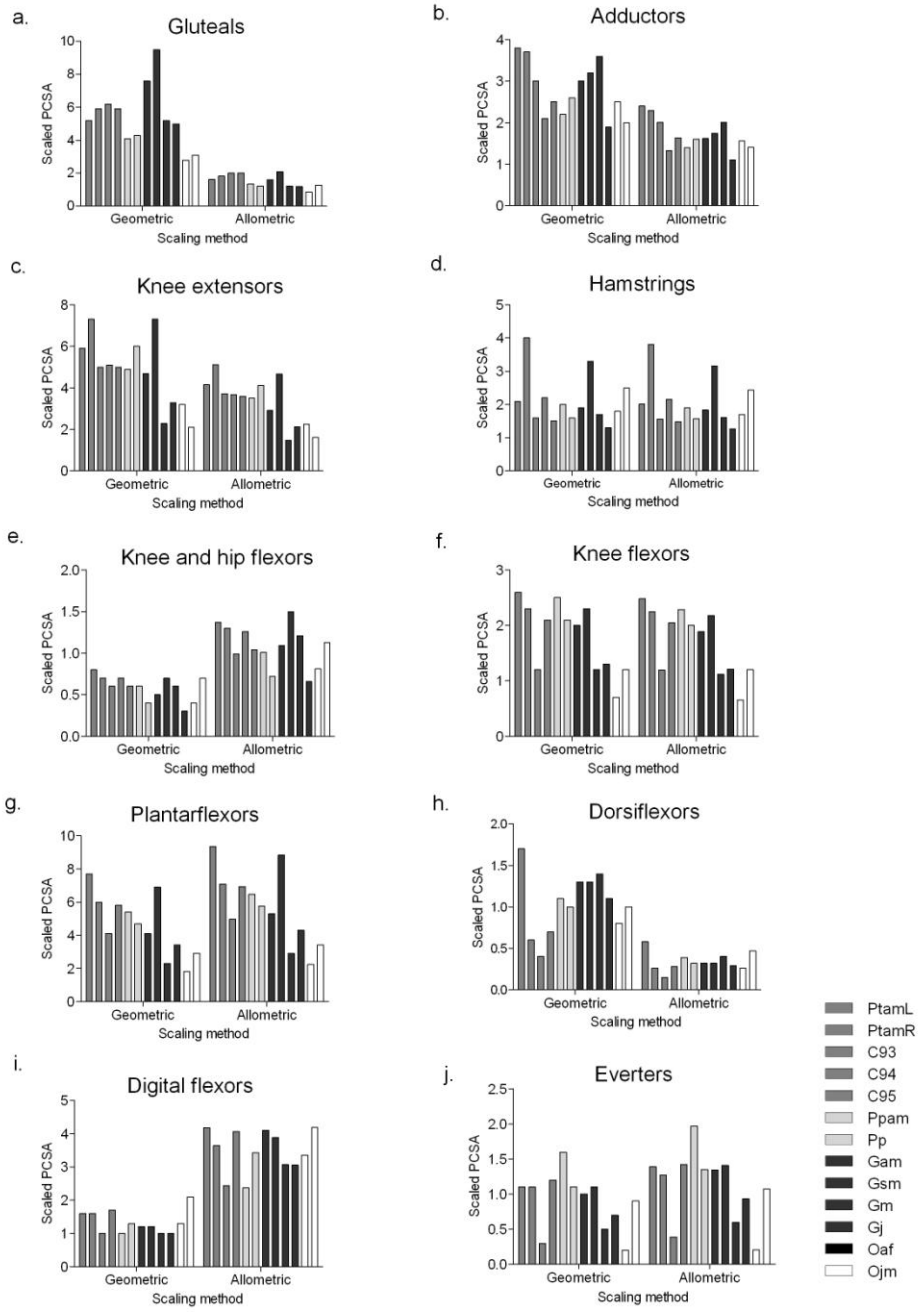


Fig. 2.4. Comparison of raw PCSA data scaled using both geometric and individual group allometric exponents. a. gluteal muscle group $M^{0.97}$ (data for chimp 93 not available); b. adductors $M^{0.79}$, c. knee extensors $M^{0.76}$, d. hamstrings $M^{0.68}$, e. knee and hip flexors $M^{0.52}$, f. knee flexors $M^{0.68}$, g. plantarflexors $M^{0.62}$, h. dorsiflexors $M^{0.94}$, i. digital flexors $M^{0.43}$, j. everters $M^{0.62}$. Figures f-j do not include data from PtsmR.

2.3.3 GLM analysis

Results for the most significant GLM models are presented in Table 2.6. In all GLM models body mass alone explained the largest proportion of the variation in belly mass for all muscle groups, except for the knee extensors and plantarflexors, where both species and body mass had a significant main effect. In the case of the knee extensors, Tukey's post-hoc test identified no significant difference between species pairs, although Figure 2.5a shows that the orangutans appear to have a smaller belly mass compared to the other species, in particular bonobos and chimpanzees. In the plantarflexors Tukey's post-hoc analysis revealed a significant difference between chimpanzees and orangutans (Tukey, $p = 0.0288$), orangutans possessing a significantly smaller belly mass than chimpanzees (Fig. 2.5b). From Figure 2.5b, the bonobos also appear to have a similar mean to the chimpanzees, although their confidence interval range was greater. The gorillas had belly masses more similar to those of the orangutans than to the other species in both the knee extensors and plantarflexors.

Table 2.6. Results from GLM models for hindlimb muscle groups

Muscle group	Muscle belly mass			Muscle fascicle length			Muscle PCSA		
	$F_{\text{degrees of freedom}}$	R^2	p	$F_{\text{degrees of freedom}}$	R^2	p	$F_{\text{degrees of freedom}}$	R^2	p
Proximal									
Gluteals	$120.2_{1,11}$	0.92	<0.001	$22.86_{1,9}$	0.71	0.001	S: $4.65_{3,11}$	0.92	0.043
							B: $13.13_{1,11}$	0.92	0.008
Adductors	$69.52_{1,11}$	0.86	<0.001	$11.57_{1,11}$	0.49	0.007	$69.97_{1,11}$	0.86	<0.001
Knee extensors	S*: $43.6_{3,11}$	0.90	0.050	$10.8_{1,11}$	0.47	0.008	$19.12_{1,11}$	0.62	0.001
	B: $18.24_{1,11}$	0.90	0.004						
Hamstrings	$69.23_{1,11}$	0.86	<0.001	$5.62_{1,11}$	0.30	0.039	$37.77_{1,11}$	0.77	<0.001
Knee and hip flexors	$50.39_{1,11}$	0.82	<0.001	$20.62_{1,11}$	0.64	0.001	$22.15_{1,11}$	0.66	0.001
Distal									
Knee flexors	$25.25_{1,11}$	0.69	0.001	$0.11_{1,11}$	0.00	0.752	$13.32_{1,11}$	0.53	0.004
Plantarflexors	S: $5.50_{3,11}$	0.87	0.029	$2.99_{1,11}$	0.15	0.114	$9.96_{1,11}$	0.45	0.010
	B: $9.94_{1,11}$	0.87	0.016						
Dorsiflexors	$71.29_{1,11}$	0.86	<0.001	$0.36_{1,11}$	0.00	0.562	$37.43_{1,11}$	0.77	<0.001
Digital flexors	$37.79_{1,11}$	0.77	<0.001	$0.03_{1,11}$	0.00	0.875	$23.36_{1,11}$	0.67	0.001
Everters	$13.72_{1,11}$	0.54	0.004	$4.07_{1,11}$	0.22	0.071	$4.66_{1,11}$	0.25	0.056

*Best model included both species (S) and body mass (B) as significant main effects

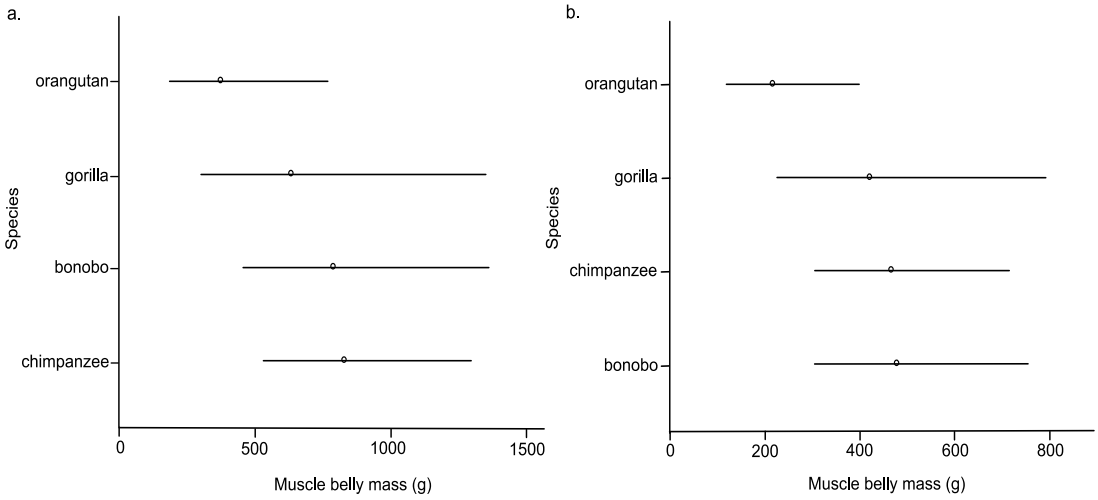


Fig. 2.5. Results from Tukey's post-hoc tests displaying mean values and 95% confidence intervals for the muscle belly mass (g) for the different species. Values presented are back-transformed from logged data. a. knee extensor belly mass. b. plantarflexor belly mass.

For fascicle length significant models were found for all proximal muscle groups, but none of the distal muscle groups. For the proximal muscles, species was not found to be significantly related to fascicle length. Instead the majority of variation was accounted for by body mass (Table 2.6), although the model fit (R^2) was rather low for the hamstrings, knee extensors and adductors. The lack of significance in the distal muscle group models indicates that there is no significant linear relationship between muscle fascicle length and body mass for these muscle groups. All PCSA models were significant, except that for the everters. Body mass explained the largest proportion of the variation in all cases, except for the gluteals, where both species and body mass had a significant effect. Tukey's post-hoc test again revealed a significant difference between chimpanzees and orangutans (Tukey, $p = 0.0372$), with orangutans having a significantly smaller PCSA than chimpanzees (Fig. 2.6). From Figure 2.6 it can be seen that the difference between the gorillas and orangutans was also close to significance, the mean being close to that of the chimpanzees (although the confidence interval range was larger). In

this instance the bonobos were more similar to the orangutans than to the other species (Fig. 2.6).

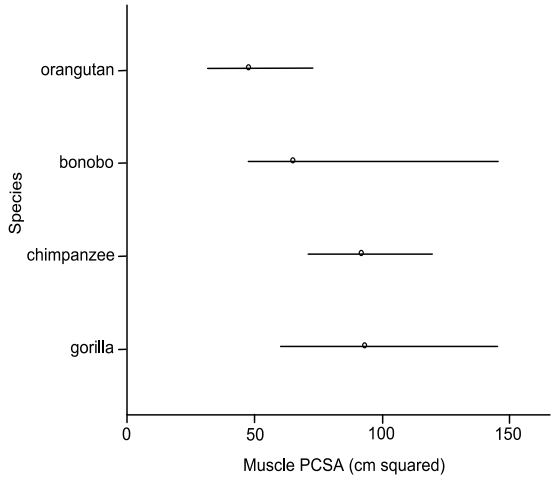


Fig. 2.6. Results from Tukey's post-hoc tests displaying mean values and 95% confidence intervals for gluteal PCSA for the different species. Values presented are back-transformed from logged data.

2.4 Discussion

2.4.1 Morphological variations

Variations in morphology may be expected between individuals and between species, even if their general body patterns are similar. In this study, scansorius was only present in the adult orangutan (Oaf). Scansorius is generally more common in orangutans than in other apes (Sigmon, 1969; Payne et al., 2006) and this is probably related to higher levels of arboreality in orangutans, as scansorius may provide an increased ability to rotate the thigh (Sigmon, 1974). The presence of the plantaris muscle in the chimpanzee (Ptsm) and bonobo (Ppam), but not in the gorillas (Gam and Gsm) or the orangutan (Oaf) also agrees with other studies, since it has been found to be absent in ~10% of humans, ~39% of chimpanzees, ~95% of

orangutans and ~99% of gorillas (Langdon, 1990). Variations in the structure of the muscle bellies and points of insertion of the digital flexor muscles are also relatively common; in particular, the presence of an additional digital flexor muscle (termed flexor digitorum fibularis in this study), in addition to flexor digitorum longus and flexor hallucis longus, in the orangutan has been described before by Sonntag (1924) and Schwartz (1988), where the flexor hallucis muscle was described as consisting of two distinct bellies, inserting onto digits three and four, one of the which could be the additional belly described here.

2.4.2 Scaling exponents and muscle architecture

The concept of geometric similarity between species has been used in previous comparative studies of ape muscle architecture (e.g. Thorpe et al., 1999; Payne et al., 2006; Oishi et al., 2008, 2009; Channon et al., 2009; Michilsens et al., 2009). While this may be appropriate in instances where comparisons are between individuals of the same species and age-sex class, some authors have argued that it is unlikely to be the most appropriate method to compare different species (Alexander et al., 1981; Schmidt-Nielsen, 1984). In general our results support the latter argument, since the regression analyses showed that the relationships between the physiological variables and body mass in great apes were better described by allometric than by geometric scaling.

Previous studies have examined the allometric scaling of hindlimb muscle architecture in mammals, including primates (Alexander et al., 1981; Pollock and Shadwick, 1994). The mean allometric scaling exponent obtained for hindlimb muscle belly mass in the present

study ($M^{0.85}$) was lower than those obtained in previous primate studies: $M^{1.05}$ (Alexander et al., 1981; Payne et al., 2006); $M^{0.98}$ (Pollock and Shadwick, 1994), and the mean allometric scaling exponent obtained for hindlimb PCSA in this study ($M^{0.70}$) was also lower than the value obtained elsewhere: $M^{0.80}$ (Alexander et al, 1981); $M^{0.88}$ (Pollock and Shadwick, 1994). However, our values still indicate that both scale with positive allometry, which reflects the ability of muscles of the larger animals to exert disproportionally greater forces. In particular the gluteals and dorsiflexors had the largest PCSA scaling exponents, indicating their ability to produce greater forces than the other muscles for any given body mass (Pollock and Shadwick, 1994). This may reflect the importance of vertical climbing in the non-human great ape locomotor repertoire, where powerful gluteal muscles provide propulsion (Sigmon, 1972; Stern and Susman, 1981) and there is a high level of force required when the ankle is dorsiflexed during push off (Myatt; pers. obs, chimpanzees and orangutans).

Previous studies have found wide variation in the scaling exponents for fascicle length: e.g. $M^{0.05}$ and $M^{0.24}$ in Pollock and Shadwick (1994); $M^{0.30}$ and $M^{0.17}$ for the proximal and distal hindlimb respectively in Alexander et al. (1981), and $M^{0.30}$ and $M^{0.34}$ for the proximal and distal hindlimb in Payne et al. (2006). The exponents for fascicle length from our study overlapped with these values (mean: $M^{0.15}$; proximal: $M^{0.20}$; distal: $M^{0.07}$). The scaling of fascicle length with negative allometry, and the lack of a significant relationship with body mass in some instances, in particular for the distal muscle groups, indicates that these muscles will likely have disproportionally shorter fascicle lengths in larger animals. This likely reflects the increased amount of external tendon length in the distal limb (Ker, 1993).

From this, it can be seen that although the exponents from other studies (Alexander et al., 1981; Pollock and Shadwick, 1994), and within this study, may be similar in range, there is a large amount of variation between them, and even a small difference in exponent can affect results substantially (Schmidt-Nielsen, 1984 and see Figure 2.2). The magnitude of the exponents used for fascicle length and PCSA, in particular, influences interpretations of the maximum speed of shortening and muscle forces that different individuals and/or species can exert, and in turn thus influences conclusions drawn about the interactions between animals and their habitat.

The extent of variation between the right and left sides of subject Ptsm from the scaled data may be related to limb dominance during locomotion (see Carlson, 2006). A difference was most strongly apparent in the knee extensors and hamstrings, with the PCSA results indicating that the right limb muscles were able to produce more force than the left (knee extensors 18.86% more; hamstrings 47.14% more). These muscles make up the bulk of the thigh and are involved in both knee extension and flexion, important during behaviours such as vertical climbing and quadrupedalism. Limb dominance is common in humans (see Sadeghi et al., 2000) and the increased ability of limb muscles on the right side to produce more force in Ptsm may therefore reflect the use of this dominant limb for propulsion, and the non-dominant limb for stabilisation (Sadeghi et al., 2000); although a much larger sample size is needed to investigate this possibility further.

The extensive intra-specific variation may have been due to the multiple age-sex classes represented for each species, as there were males and females, juveniles and adults within the

data-set. Field and captive studies suggest that juveniles may be more active or perform different behaviours compared to adults (e.g. Hunt, 1992; Thorpe et al, 2009; Hanson et al, in prep) which may result in differences in morphology, as were observed between the adult and juvenile orangutan in this study. The greater ability of the juvenile to produce force across a number of their muscle groups possibly reflects an increased use of arboreal-type supports and behaviours in the captive environment, and generally increased amount of activity, compared to adults (Hanson et al., in prep). Depending on the exponents used, there was either an increase in the magnitude of the difference between individuals when scaled allometrically, or a decrease (depending on whether the exponent was positively or negatively isometric) This further highlights the fact that the interpretation of species differences and of the relationship between morphology, behaviour and habitat may be influenced by the choice of scaling exponent. However, although some individuals stood out in comparison to the others, there were relatively few major differences apparent between the different species. This recalls the finding of Payne et al. (2006) that the non-human apes were generally characterised by longer fascicle length and smaller PCSAs when compared to humans, reflecting their need to produce moderate forces over a range of joint motions during arboreal locomotion (Thorpe et al., 1999).

2.4.3 Species comparisons using statistical analyses

GLMs on log-transformed data were found in this study to identify species differences more clearly than was possible through the visual analysis of scaled data. The results suggest that the variation in muscle belly mass observed between different non-human great ape species is predominantly the result of differences in body mass rather than species, although a much

larger sample size would be needed to confirm this, as the small sample size herein resulted in wide confidence intervals and may reduce the power of the statistical model (Grafen and Hails, 2002).

Tukey's post-hoc test for the plantarflexors highlighted a significant difference between the orangutans and the chimpanzees, the orangutans having the lightest muscles of all species, and the chimpanzees and bonobos the heaviest; however, there was no significant difference between the PCSAs, and thus the force production capacity, of these muscles. Species did not have a significant effect on fascicle length and non-significant models resulted for all distal muscle groups, indicating that neither species nor body mass explained any of the variation observed in these muscles. These results accord with those from the regression analysis, and seem to reflect the importance of foot and toe control, during arboreal locomotion and other behaviours, such as feeding (Thorpe et al., 1999; Payne et al., 2006). PCSA differed significantly between species only in the case of the gluteals, where orangutans, with the smallest PCSA of all species, differed significantly from the chimpanzees, with the gorillas being more similar to the chimpanzees and the bonobos to the orangutans. The smaller PCSA in the orangutan gluteals probably reflects their increased need for mobility around the hip joint compared to the more terrestrial chimpanzees during their more frequent use of arboreal behaviours. As bonobos are also more arboreal than either chimpanzees or gorillas (Doran, 1993; Remis, 1995), this further supports the above interpretation of the pattern of variation observed. Kinematic differences between the species during the same behaviours may also be influential, for example in vertical climbing, where orangutans use a greater range of motion at the hip (Isler, 2005).

2.4.4 Concluding remarks

Overall, from this study, the differences in hindlimb muscle architecture between the different species appear to be small, and non-significant in most cases, both from the scaled data and the GLMs. This seems to suggest that even though the non-human great apes live in different habitats and perform locomotor behaviours in different proportions, their basic functional morphology remains very similar. This likely reflects their close evolutionary history, their ability to use a wide variety of locomotor modes and substrates, and the fact that their locomotion is characterised overall by orthograde positional behaviours (Thorpe and Crompton, 2006; Crompton et al., 2008). However, macro-architecture may not provide the whole picture, as there may be further variation in the micro-architecture (i.e. the proportions of different muscle fibre types) which may further modulate the functional capability of a muscle (e.g. Acosta and Roy, 1987; see Chapter 4).

The methods of analysis in this study have both benefits and disadvantages for comparing the data. The use of allometric exponents to normalise data enables a visual comparison of the different individuals, however, it is difficult to accurately compare species due to the large amount of intra-specific variation in the present study using this method. The use of GLMs, on the other hand, enables significant differences between species to be established, but is more appropriate for larger sample sizes. Furthermore, although the differences between the species may appear small from both forms of analysis, the magnitude of the difference may not need to be that large to have a functional impact, and this should be considered when interpreting the data.

As sample sizes of primate cadaveric material increase, there will be exciting opportunities to move beyond broad-based comparisons of maximum musculo-skeletal ability, which rather inevitably show that animals are designed for the behaviours we already know they exhibit, towards a more refined analysis of the subtleties of the relationship between form and function. However, in the case of primate data, it may take many years to collate a sufficient amount of data to allow robust statistical analyses, and until such a time, we recommend exploration of the data using multiple methods to provide a more comprehensive comparison of data.

CHAPTER 3

FUNCTIONAL ADAPTATIONS IN THE FORELIMB MUSCLES OF NON-HUMAN APES

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The maximum capability of a muscle can be estimated from simple measurements of muscle architecture such as muscle belly mass, fascicle length and physiological cross-sectional area (PCSA). While the hindlimb anatomy of the non-human apes has been studied in some detail, a comparative study of the forelimb architecture across a number of species has never been undertaken. Here we present data from chimpanzees, bonobos, gorillas, orangutans and a gibbon to ascertain if, and where, there are functional differences relating to their different locomotor repertoires and habitat usage. We employed a combination of analyses including allometric scaling and General Linear Models to explore the data, as the sample size was relatively small and from a range of age-sex classes. Overall, it appears that the non-human apes do not vary greatly across the different physiological variables, even though they perform different locomotor behaviours at different frequencies. Therefore, it would appear that the time spent performing a particular behaviour does not necessarily correlate with the extent of its influence on the design of the musculoskeletal system. However, significant differences in wrist extensor musculature between chimpanzees and gorillas appear to provide strong support for the argument that knucklewalking is mechanically distinct (and therefore probably non-homologous) in the African apes, and contrariwise, the overall consistency of musculoskeletal morphology both between and within the Asian and African apes strengthens the case for a shared evolutionary origin for orthogrady under compressive and/or suspensory loading in the great apes.

JPM conducted some of the data collection; analysed the data and wrote the manuscript. RHC assisted with data collection and aided in the writing of the manuscript. RCP provided some of the raw data and KI, EEV, MMG and DA assisted RCP with the collection of her raw data. RS assisted with the collection of all data. SKST assisted with data collection, discussion of the statistical analysis and aided in the writing of the manuscript.

3.1 Introduction

It is generally agreed that the living apes form a biological lineage defined by characters of the locomotor system (trunk and limbs) rather than the cranial and dental features which define many other mammalian groups (see review in Crompton et al, 2008). Due to interest in the evolution of hominin bipedalism, morphological studies of the apes have frequently focused on hindlimb anatomy (e.g. Thorpe et al., 1999; Carlson, 2006; Payne et al., 2006; Channon et al., 2009), forelimb muscle architecture being studied to a lesser extent and in fewer species (e.g. chimpanzee: Thorpe et al., 1999; Carlson, 2006; orangutan and chimpanzee: Oishi et al., 2008, 2009; gibbon: Michilsens et al., 2009). Non-human apes are however, considered to be united predominantly by shared features in the thorax and upper limb, such as short lumbar spines, craniocaudal increase in area of lumbar centra, broad ilia, broad, shallow trunks, dorsally placed scapula, and shoulder joints adapted for highly abducted arm postures (e.g. Larson, 1998; Ward, 2007). While past comparative studies of primate forelimb anatomy have been carried out under a paradigm that held that apes were united by their use of brachiation (e.g. Ashton and Oxnard, 1962a, b), fossil evidence (from eg. *Pierolapithecus*, Moyà-Solà al. 2004) now suggests that forelimb suspensory locomotion arose independently in several ape lineages, while an increasing number of field studies have revealed that it is generalised orthograde clambering where the trunk is upright and both fore- and hindlimbs are used in varying degrees to support body mass in suspensory or compressive loading regimes (e.g. Hunt, 1991; 1996; Fleagle, 1999), which is the locomotor behaviour that characterises the non-human apes (e.g. Hunt et al.,1992; Doran, 1993a,b ; Fleagle, 1999; Thorpe and Crompton, 2006; reviewed in Crompton et al., 2008). A comparison of the functional morphology of the forelimbs could therefore greatly add to our understanding of locomotor diversity in the hominoids and its evolution.

The measurement of basic anatomical parameters including muscle belly mass and muscle fascicle length enables functional parameters such as muscle physiological cross-sectional area (PCSA) to be estimated. Fascicle length reflects the number of sarcomeres in series; and the longer the fascicle length, the greater the maximum shortening velocity of the muscle fascicles (see Wickiewicz et al., 1984; Thorpe et al., 1999). PCSA, on the other hand, reflects the number of sarcomeres in parallel, and provides an indication of the maximum force a muscle can produce (Sacks and Roy, 1982; Zajac, 1992).Together fascicle length and PCSA enable the maximum capability of a muscle to be determined (e.g. Thorpe et al., 1999; Carlson, 2006; Payne et al., 2006). By relating these measurements of muscle architecture (anatomical form) to the behaviours performed by the animal (function and performance), we can explore whether subtle differences exist in non-human ape adaptations to their habitats.

Even though the locomotor repertoires of the great apes overlap, the proportions of the different behaviours and their kinematics do differ between species and we might expect this to impact on their morphology. One of the major behavioural differences is the percentage of time spent in the arboreal milieu. The Asian apes (the gibbons and orangutans) are predominantly arboreal, rarely coming to the ground at all (although Bornean flanged male orangutans will travel on the ground; see Galdikas, 1988), as reflected by their much longer forelimbs in comparison to body size compared to the nonhuman African apes (chimpanzees, bonobos and gorillas). African apes primarily use terrestrial quadrupedalism when travelling (89.9% of locomotor behaviours in chimpanzees; 35.3% in bonobos and between 64.4 and 96% in gorillas: see Hunt, 2004), and only enter the canopy predominantly to feed (e.g. Hunt, 1992). We might therefore expect that the greater use of arboreal locomotor behaviours in gibbons and orangutans would be reflected in their morphology e.g. larger digital flexor

muscles with longer muscle fascicles, which might be beneficial when gripping variously-angled supports in suspension (Alexander et al., 1981).

In contrast, we might expect that non-human African ape morphology will exhibit stronger adaptations to their use of terrestrial quadrupedalism. However, as primates, chimpanzees are 'hindlimb driven' when quadrupedal, as opposed to 'forelimb driven' as are non-primate quadrupedal mammals such as cats (see Larson and Stern, 1987; Vilensky, 1989). In the African apes, therefore, the forelimbs play more of a support role, as opposed to being used for propulsion and braking (Vilensky, 1989) or even steering (Li et al., 2004). Therefore, rather than showing specific adaptations to quadrupedal walking in their forelimbs, we might expect that the nonhuman African apes would simply show less substantial adaptations in their forelimbs to arboreal behaviours than the Asian apes. African apes do use suspensory behaviours, but more frequently as static postural activity during feeding, where the stresses will be lower than those for suspensory locomotion. As all non-human apes use vertical climbing to a greater or lesser extent to access food in the canopy, one would expect, for example all to show adaptations for production of greater force in the elbow flexors for pulling-up (e.g. Isler, 2005). However, kinematically, vertical climbing is performed in a distinct manner in the African apes compared to orangutans (Thorpe and Isler, 2003; Isler, 2005). We would therefore expect that such differences would be reflected in the forelimb architecture of the different species. The overall aim of this study, therefore, was to compare the forelimb muscle architecture of all the non-human great apes, to expand our understanding of the relationship between form and function in these species and further our knowledge of the extent and evolution of locomotor diversity in the hominoids.

3.2 Materials and methods

The material obtained for this study was comprised cadavers of one chimpanzee (*Pan troglodytes:* Ptsm); two bonobos (*Pan paniscus:* Ppam, Pp); five gorillas (*Gorilla gorilla gorilla:* Gsm, Gam,Gp, Gj; *Gorilla gorilla graueri*: Gm); three orangutans (*Pongo abelii:* Oaf, Ojf, Ojm) and one gibbon (*Hylobates lar*: Hlf) (See Table 3.1 for subject information). Additional data for three chimpanzees (chimps 93, 94 and 95) from Thorpe (1997) were also incorporated. Incorporating data collected from previous studies is essential in studies of this nature as individual data sets are often very small because of the problems of obtaining primate cadavers and combining datasets enables more robust statistics to be performed. Cadavers were obtained from The Zoological Society, London (Ptsm, chimp 95), The North of England Zoological Society (chimp 93, chimp 94, Gj), Twycross Zoo (Gsm, Gam), Apenheul Zoo (Ppam), The Royal Zoological Society of Antwerp (Pp, Gm), the Anthropological Institute and Museum, Zurich (Ojf, Ojm, Hlf and Gp) and Paignton Zoo (Oaf). All specimens had been eviscerated during autopsy and were kept fresh-frozen until needed.

Table 3.1 Subject information

Subject	Species	Sex	Body mass (kg)	Age at death (years)	Cause of death	Forelimb dissected
PtsmL[1]	*P. troglodytes*	M[2]	50.20	11	Group violence	L
PtsmR		M	50.20	11	Group violence	R
Chimp 93		M	27.60	Sub-adult	PE[3]	L
Chimp 94		M	41.70	Adult	Euthanized	L
Chimp 95		M	37.00	6	Peritonitis	L
Ppam	*P. paniscus*	M	41.92	22	Euthanized	L
Pp		M	64.00	29	Cardiovascular	L
Gsm	*G. g. gorilla*	M	152.00	18	BH	L
Gam		M	175.00	30	Cardiovascular	L
Gp		M	130.00	35	Cardiovascular	?
Gj	*G. g. graueri*	M	120.00	30	Cardiovascular	?
Gm		M	120.00	33	Cardiovascular	L
Oaf	*P. abelii*	F	54.00	45	Euthanized	R
Ojf		F	12.50	5	Viral	?
Ojm		M	18.70	6	Cardiovascular	?
Hlf	*H. lar*	F	4.60	16	Viral	?

[1]Limbs on both the left and right side were available for dissection from this individual and therefore two different subject codes are given to distinguish between them.

[2]M: male, F: female

[3]Abbreviations: PE indicates death due to a pulmonary embolism, BH indicates death due to a brain haemorrhage.

3.2.1 Anatomical measurements and functional groupings

Muscle fascia were removed and muscles were separated and identified before being removed systematically with complete tendons attached. Points of bony origin and insertion were recorded. Muscle-tendon unit lengths were measured, including separate measurements for external tendon lengths at the origin and insertion, and muscle belly length. External tendon length was measured as the distance from the either the most proximal (tendon of origin) or distal (tendon of insertion) muscle fibres to the point of tendon attachment to the bone. Any external tendon was then removed and muscle belly mass (including internal tendons)

recorded. Finally, the muscle belly was cut, either along the line of the internal tendon (for pennate muscles), or along the belly (for parallel fibred muscles) to reveal the full length of the muscle fibres. Three measurements of muscle fascicle length were made at different locations throughout the belly. Muscle fascicle length assesses the length of the bundle of muscle fibres which are visible to the naked eye. Muscle mass was measured to the nearest 0.1 g, and tendon mass to the nearest 0.01 g. All lengths were measured to the nearest millimetre using a metal rule.

To provide an estimate of maximum muscle force production, physiological cross-sectional area (PCSA) was calculated using the equation:

Equation 3.1 $$PCSA = m/\rho l$$

where m is muscle belly mass in grams, ρ is the density of fresh muscle (1.06 g cm^{-3}, Mendez and Keys, 1960) and l is muscle fascicle length in cm. In apes the angle of the fascicles to the tendon (pennation angle) is generally less than 30^{o} in both fore- and hind-limb muscles (Thorpe et al., 1999), thus $\cos\theta$, normally present in this equation ($PCSA = (\cos\theta \times m)/\rho l$) is approximately one and can be omitted (also discussion in Calow and Alexander, 1973).

To enable comparisons, muscles were grouped according to their primary functions, based on previous studies of ape muscle anatomy (Swindler and Wood, 1973; Michilsens et al., 2009; see Table 3.2 for groupings). Obtaining measurements for muscles at the shoulder was problematic as often these muscles could not be separated into their separate functional units. For example, the deltoid muscle consists of three components arising from three different

points on the shoulder girdle that insert together onto the shaft of the humerus. Each part performs a different action (see Ashton and Oxnard, 1962 for description of primate deltoid), but it was not possible to anatomically separate the functional units and as a result the deltoid was removed and measured as one muscle. Such muscles were therefore placed into multiple functional groups, even though only a proportion of the muscle was likely involved in each separate function. Estimating the proportion of each muscle that contributed to a specific function was not a viable option: without detailed EMG analysis of the different regions of a muscle we cannot be sure what proportion contributes to different functions, and indeed such relationships may be more complex than expected (e.g. Michiels and Bodem, 1992). Intrinsic hand muscles were not included in the analysis, as they were not measured in the majority of the subjects. Furthermore, dissection of the shoulder girdle was not complete in all species, due to damage during evisceration (particularly of the pectoral muscles). Therefore, total values for the shoulder flexors, shoulder adductors and shoulder rotators were underestimated as, for example, the pectoralis major contributes to each of these groups. In cases where we were not able to sample all muscles in a muscle group for a particular individual, those individuals were excluded from the analysis of that particular muscle group.

To obtain overall values for muscle groups, muscle belly masses and PCSA values within a group were simply added together. However, muscle fascicle length was calculated as a weighted harmonic mean to take the different sizes of the muscles in a group into account, using the equation:

Equation 3.2 $$L = \sum m_j / \sum (m_j / l_j)$$

Where L is the group fascicle length, for a group where the jth member has a mass m_j and a fascicle length of l_j (Alexander et al., 1981).

Table 3.2. Functional muscle groups for the forelimb

Muscle Group	Muscles
Shoulder rotators[1]	Latissimus dorsi, infraspinatus, teres major, teres minor, subscapularis, deltoid
Shoulder adductors	Coracobrachialis, teres major
Shoulder abductors	Deltoid, supraspinatus
Shoulder flexors	Deltoid, biceps brachii, coracobrachialis
Shoulder extensors	Triceps brachii, teres major, latissimus dorsi, deltoid
Elbow flexors	Biceps brachii, brachialis, brachioradialis
Elbow extensors	Triceps brachii, dorsoepitrochlearis, anconeus
Supinators	Supinator
Pronators	Pronator teres, pronator quadrates
Wrist flexors	Flexor carpi ulnaris, flexor carpi radialis, flexor digitorum profundus
Wrist extensors	Extensor carpi ulnaris, extensor carpi radialis brevis, extensor carpi radialis longus
Digital flexors	Flexor pollicis longus, flexor digitorum superficialis, flexor digitorum profundus, abductor pollicis longus
Digital extensors	Extensor pollicis brevis, extensor digitorum communis, extensor pollicis longus, extensor digiti minimi, extensor indicis

[1] for description of shoulder muscle group actions see Michilsens et al. (2009).

3.2.2 Data analysis

For species comparisons we have previously recommended both normalising the data using allometric scaling exponents, and using general linear models with body mass as a covariate, to explore whether species differences were present (chapter 2). This approach was also used here, with regression analysis of log-transformed data performed initially by plotting each physiological variable (belly mass, fascicle length and PCSA) against body mass (kg) using Minitab® version 15 (USA). We thus intended to establish the form of relationships, rather

than assuming geometric similarity as has frequently been done in previous studies (see chapter 2 for discussion).

From regression analysis, the relationships between body mass and belly mass, fascicle length and PCSA were found to be allometric in form for all functional muscle groups. Allometric scaling exponents were determined based on the equation $Y = aM^b$, where Y is the physiological variable, M is body mass in kg, a and b are constants, and b is the scaling exponent (see Alexander et al., 1981; Schmidt-Nielsen, 1984; Pollock and Shadwick, 1994). Exponents for the individual muscle groups were calculated, as were exponents for the proximal and distal forelimb muscles and for the limb as a whole. Mean scaling exponents were established from the individual group values. Raw data were normalised using the individual muscle group scaling exponents for belly mass, fascicle length and PCSA.

3.2.3 General Linear Models

GLMs (with type III hypotheses) using log-transformed data, with body mass as a covariate, were employed to compare muscle belly mass, fascicle length and PCSA between the different species again using Minitab 15. To achieve a model of best fit the main effects 'species' and 'body mass' and the interaction 'species*body mass' were first included. Backward elimination was then used to remove each non-significant term (significance taken at the $p = 0.05$ level), one at a time, until the best fitting model remained (see Grafen and Hails, 2002). In cases where either the interaction and/or species were found to have a significant effect, Tukey's post-hoc tests were performed to establish which species were significantly different ($p = 0.05$). Multiple individuals of each species are needed to adopt this

approach. Therefore, GLMs could only be used to compare chimpanzees, bonobos, gorillas and orangutans, as data from multiple gibbons were not available. Furthermore, models for the shoulder extensors, shoulder abductors and shoulder rotators could not be established as data available were reduced to one individual per species in these groups, due to missing data. Missing data also resulted in: Ptsm, Gp and Gj being excluded from the supinator model; chimp 93 being excluded from the shoulder flexor model and Gp and Gj being excluded from the shoulder adductor model.

3.3. Results

3.3.1 Descriptive anatomy

Raw data from all subjects are presented in appendix A. The general gross anatomy of non-human ape arm and shoulder muscles is similar to that of humans, except for the presence of an additional muscle, dorsoepitrochlearis, in the upper arm of non-human primates, which is only present as fascia in humans (Ashton and Oxnard, 1962; Oxnard and Franklin, 2008). The qualitative anatomy of the ape forelimb has been described elsewhere (e.g. Sonntag, 1924; Miller, 1952; Ashton and Oxnard, 1962; Kimura and Takai, 1970; Swindler and Wood, 1973; Gibbs et al., 2002; Michilsens et al., 2009) and thus this section is limited to the description of those anomalies which are functionally important.

Biceps brachii usually arises from the coracoid process of the scapula (short head) and the supraglenoid tuberosity of the scapula (long head) in primates (Sonntag, 1924; Miller, 1952; Kimura and Takai, 1970; Swindler and Wood, 1973; Youlatos, 2000). In the orangutan Oaf,

however, the long head was monoarticular, arising from the top of the lateral side of the humerus, just below the bicipital groove. The short head originated as normal from the coracoid process of the scapula. The origin of biceps brachii in the gorillas Gsm and Gam also differed in that the tendon of the long head originated from below the supraglenoid tuberosity on the back of the scapula. Flexor pollicis longus, a separate muscle in humans, is not usually a separate muscle belly in non-human great apes, although there may be a tendon from the belly of flexor digitorum profundus to digit one (Mangini, 1960). However, a separate belly with a tendon to digit one was present in Ppam, Gam and Oaf, following the origin and insertion of flexor pollicis longus in *Homo* (Mangini, 1960). In Ppam there was also an additional tendon to digit two and the belly was more tightly fused to flexor digitorum profundus. PtsmR and Gsm also had separate bellies to flexor digitiorum profundus but rather than giving tendon to digit one, gave a tendon to digit two.

3.3.2. Scaled data

Equation components from regressions of log-transformed data for allometric scaling are given in Table 3.3 for belly mass, fascicle length and PCSA. Muscle belly masses, fascicle lengths and PCSAs for all muscle groups were found to have significant linear relationships with body mass (M). The overall mean scaling exponent for muscle mass was $M^{0.94}$, individual muscle groups ranging from $M^{0.76}$ to $M^{1.11}$, revealing that some muscle groups scaled below the exponent predicted by isometry, (i.e. $M^{1.0}$, labelled negatively isometric) and some scaled above isometry (positively isometric). The mean scaling exponent for fascicle length was $M^{0.28}$ (range: $M^{0.18}$ to $M^{0.40}$), compared to the isometric prediction of $M^{0.33}$ and PCSA was $M^{0.70}$ (range: $M^{0.56}$ to $M^{0.80}$) compared to an isometric exponent of $M^{0.67}$. Thus

exponents for fascicle length and PCSA also fall on both sides of values predicted by geometric similarity.

Table 3.3. Allometric equation constants for forelimb muscle belly mass (g)

Muscle group	**Muscle belly mass (g)**			
	a (±SE)[1]	**b (±SE)**	***R*²**	***p***
Overall				
Total	4.74 (±0.74)	0.99 (±0.18)	0.90	0.033
Proximal	4.31 (±0.33)	1.06 (±0.09)	0.97	<0.001
Distal	3.61 (±0.23)	0.78 (±0.06)	0.94	<0.001
Proximal				
Shoulder				
Rotators	2.77 (±0.38)	1.10 (±0.10)	0.95	<0.001
Adductors	1.06 (±0.29)	1.07 (±0.07)	0.94	<0.001
Abductors	2.15 (±0.47)	1.00 (±0.13)	0.88	<0.001
Flexors	2.85 (±0.30)	0.91 (±0.08)	0.91	<0.001
Extensors	2.82 (±0.23)	1.11 (±0.06)	0.98	<0.001
Elbow				
Flexors	3.06 (±0.30)	0.81 (±0.08)	0.88	<0.001
Extensors	1.89 (±0.17)	1.06 (±0.04)	0.98	<0.001
Distal				
Supinators	0.17 (±0.44)	0.92 (±0.11)	0.84	<0.001
Pronators	0.76 (±0.28)	0.84 (±0.07)	0.91	<0.001
Wrist				
Flexors	1.35 (±0.39)	0.89 (±0.10)	0.85	<0.001
Extensors	1.03 (±0.25)	0.92 (±0.06)	0.93	<0.001
Digital				
Flexors	2.90 (±0.20)	0.76 (±0.05)	0.94	<0.001
Extensors	1.21 (±0.22)	0.83 (±0.05)	0.94	<0.001
Mean exp		**0.94(±0.03)**		

[1]Equation takes the form $y = aM^b$, where M is body mass (kg) and a and b are provided above.

Table 3.4. Allometric equation constants for forelimb muscle fascicle length (cm)

Muscle group	Muscle fascicle length (cm)			
	a (±SE)[1]	**b (±SE)**	***R*²**	***p***
Overall				
Total	0.68 (±0.77)	0.27 (±0.19)	0.21	0.248
Proximal	0.67 (±0.36)	0.43 (±0.10)	0.73	0.004
Distal	1.34 (±0.30)	0.12 (±0.08)	0.13	0.150
Proximal				
Shoulder				
Rotators	1.14 (±0.15)	0.33 (±0.04)	0.93	<0.001
Adductors	1.08 (±0.27)	0.30 (±0.07)	0.60	0.001
Abductors	0.89 (±0.28)	0.32 (±0.08)	0.67	0.004
Flexors	1.30 (±0.22)	0.26 (±0.06)	0.59	<0.001
Extensors	1.10 (±0.23)	0.35 (±0.06)	0.81	0.001
Elbow				
Flexors	1.66 (±0.24)	0.23 (±0.06)	0.47	0.002
Extensors	0.84 (±0.17)	0.35 (±0.04)	0.82	<0.001
Distal				
Supinators	0.42 (±0.19)	0.22 (±0.05)	0.59	0.001
Pronators	0.44 (±0.32)	0.27 (±0.08)	0.41	0.004
Wrist				
Flexors	0.73 (±0.31)	0.26 (±0.08)	0.39	0.006
Extensors	-0.07 (±0.56)	0.40 (±0.14)	0.31	0.014
Digital				
Flexors	1.21 (±0.23)	0.20 (±0.06)	0.42	0.004
Extensors	1.22 (±0.24)	0.18 (±0.06)	0.36	0.009
Mean exp		**0.28(±0.02)**		

[1]Equation takes the form $y = aM^b$, where M is body mass (kg) and a and b are provided above.

Table 3.4. Allometric equation constants for forelimb muscle PCSA (cm^2)

Muscle group	Muscle PCSA (cm^2)			
	a (±SE)[1]	**b (±SE)**	***R²***	***p***
Overall				
Total	3.33 (±0.57)	0.74 (±0.14)	0.90	0.034
Proximal	3.19 (±0.37)	0.71 (±0.10)	0.91	0.002
Distal	2.34 (±0.32)	0.66 (±0.08)	0.86	<0.001
Proximal				
Shoulder				
Rotators	1.61 (±0.34)	0.78 (±0.09)	0.93	<0.001
Adductors	-0.28 (±0.32)	0.80 (±0.08)	0.88	<0.001
Abductors	1.20 (±0.43)	0.69 (±0.12)	0.81	<0.001
Flexors	1.50 (±0.38)	0.66 (±0.09)	0.77	<0.001
Extensors	1.64 (±0.32)	0.78 (±0.08)	0.92	<0.001
Elbow				
Flexors	1.35 (±0.38)	0.58 (±0.10)	0.70	<0.001
Extensors	0.97 (±0.24)	0.72 (±0.06)	0.90	<0.001
Distal				
Supinators	-0.31 (±0.45)	0.71 (±0.12)	0.75	<0.001
Pronators	-0.37 (±0.41)	0.72 (±0.10)	0.78	<0.001
Wrist				
Flexors	-0.10 (±0.65)	0.79 (±0.09)	0.62	<0.001
Extensors	0.12 (±0.27)	0.65 (±0.07)	0.86	<0.001
Digital				
Flexors	1.60 (±0.33)	0.56 (±0.08)	0.75	<0.001
Extensors	0.03 (±0.41)	0.65 (±0.10)	0.72	<0.001
Mean exp		**0.70 (±0.02)**		

[1]Equation takes the form $y = aM^b$, where M is body mass (kg) and a and b are provided above.

Muscle group data for fascicle length and PCSA, scaled using individual muscle-group allometric exponents, are presented in Figures 3.1 and 3.2 respectively (belly mass is not presented as the main interest in this study is the relationship between mobility and force production, rather than power output). In all species muscle fascicles were longest in the shoulder rotators and elbow flexors (i.e. the proximal muscle groups). Within the distal muscle groups, the digital flexors and extensors had the longest fascicle lengths. Overall, PCSA was greatest in the shoulder extensors and shoulder rotators and was generally greater in the proximal than the distal muscle groups. The digital flexors had largest PCSAs in distal muscle groups, and overall, the supinators and wrist extensors had the smallest PCSAs.

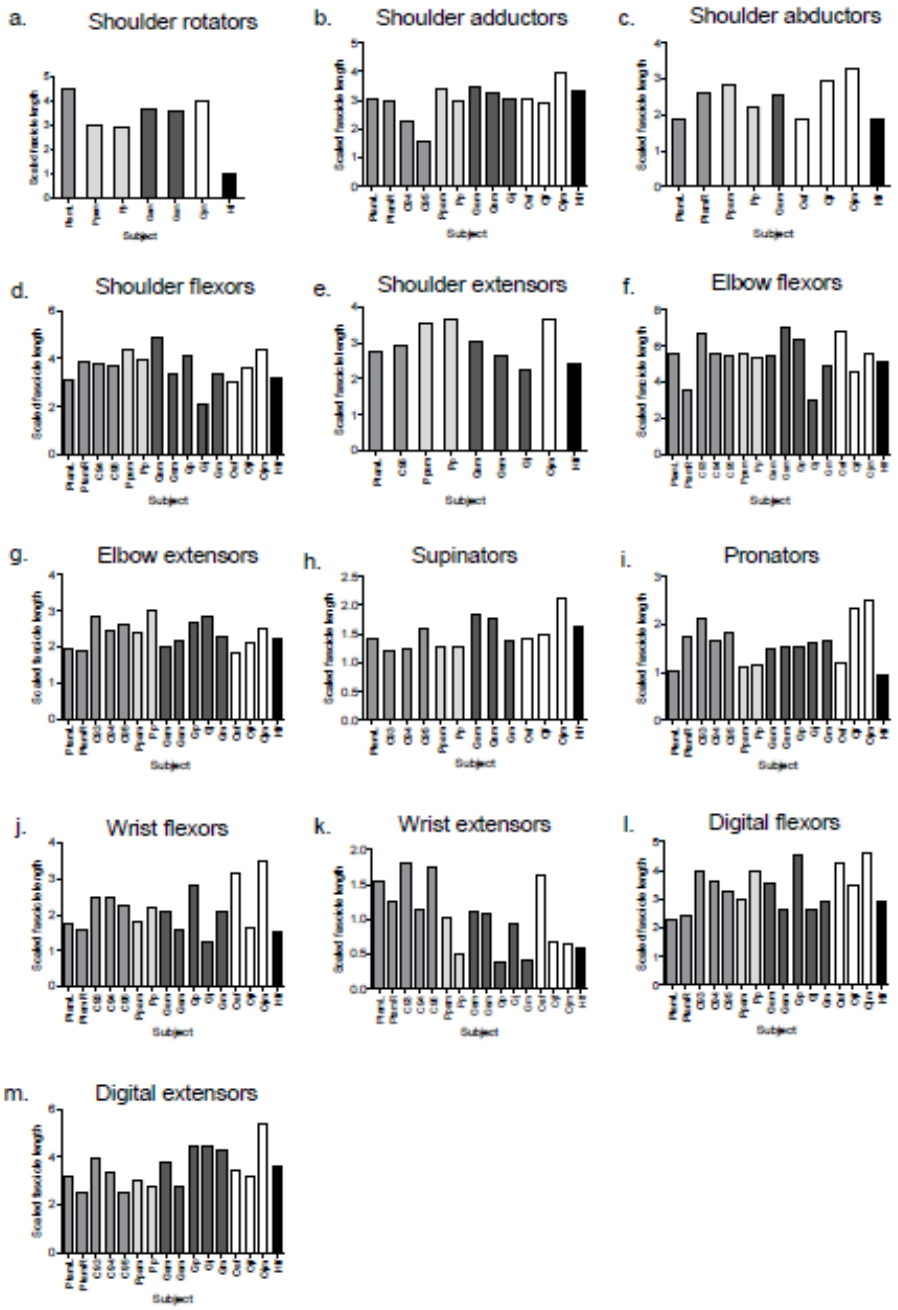

Fig. 3.1. Raw fascicle length data scaled using individual group allometric exponents. a. shoulder rotators ($M^{0.33}$), b. shoulder adductors ($M^{0.30}$), c. shoulder abductors ($M^{0.32}$), d. shoulder flexors ($M^{0.26}$), e. shoulder extensors ($M^{0.35}$), f. elbow flexors ($M^{0.23}$), g. elbow extensors ($M^{0.35}$), h. supinators ($M^{0.22}$), i. pronators ($M^{0.27}$), j. wrist flexors ($M^{0.26}$), k. wrist extensors ($M^{0.40}$), l. digital flexors ($M^{0.20}$), m. digital extensors ($M^{0.18}$). Chimpanzees are shaded in medium grey, bonobos in light grey, gorillas in dark grey, orangutans in white and the gibbon in black.

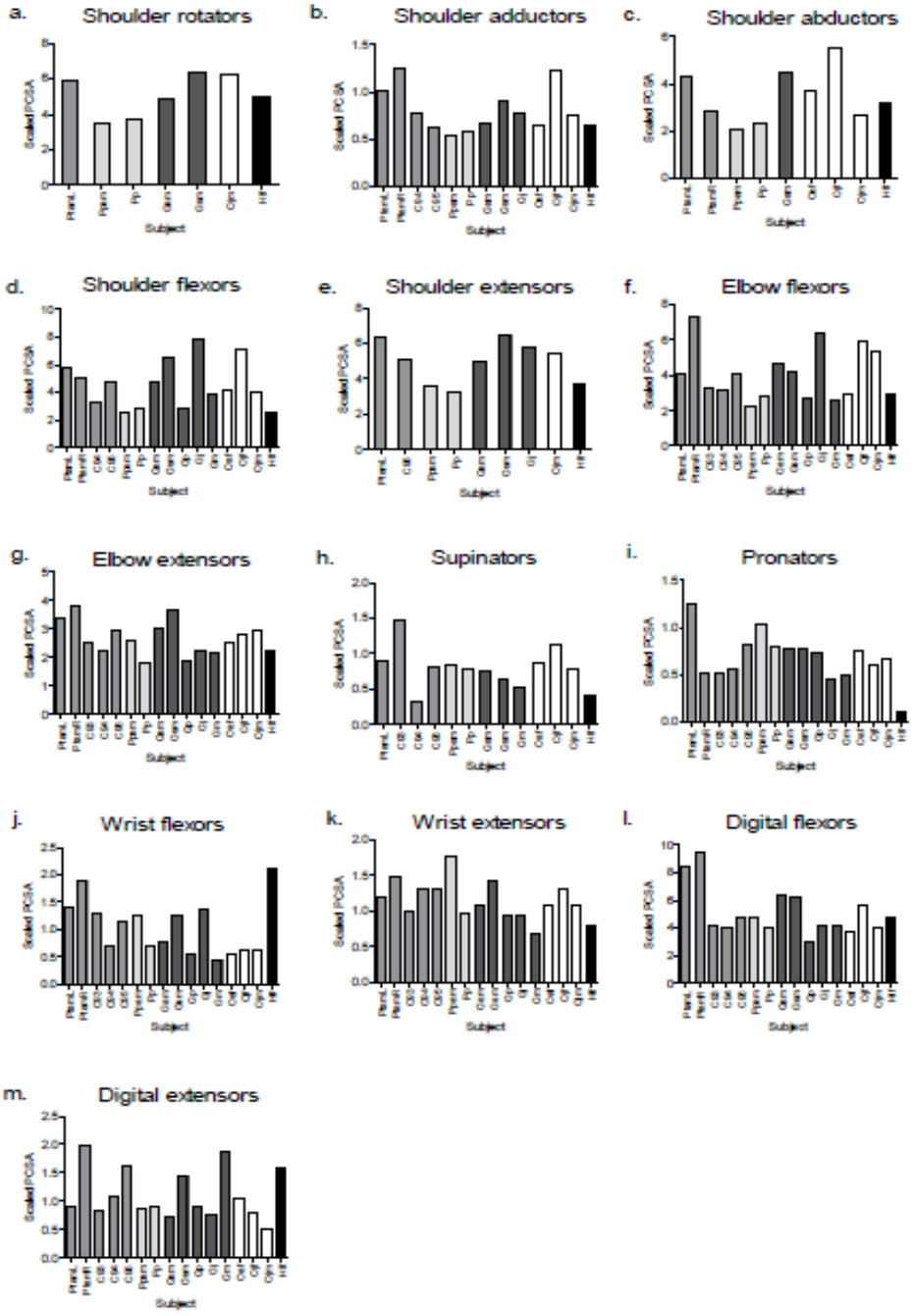

Fig. 3.2. Raw PCSA data scaled using individual group allometric exponents. a. shoulder rotators ($M^{0.78}$) b. shoulder adductors ($M^{0.80}$), c. shoulder abductors ($M^{0.69}$), d. shoulder flexors ($M^{0.66}$), e. shoulder extensors ($M^{0.78}$), f. elbow flexors ($M^{0.58}$), g. elbow extensors ($M^{0.72}$), h. supinators ($M^{0.71}$), i. pronators ($M^{0.72}$), j. wrist flexors ($M^{0.79}$), k. wrist extensors ($M^{0.65}$), l. digital flexors ($M^{0.56}$), m. digital extensors ($M^{0.65}$). Chimpanzees are shaded in medium grey, bonobos in light grey, gorillas in dark grey, orangutans in white and the gibbon in black.

The most notable feature of Figures 3.1 and 3.2, however, is the high level of intra-specific variation, which makes it difficult to ascertain whether inter-specific differences actually exist. This was particularly prevalent in the gorillas, even though they were all male and of a similar age except for Gsm (see Fig. 3.1 and 3.2; Table 3.1). For example, the juvenile orangutans (Ojf, Ojm) had slightly shorter fascicle lengths in the elbow flexors and much larger PCSAs than did the adult orangutan (Oaf). In the pronators the juvenile orangutans also had longer fascicles than the adult orangutan, but there was no substantial difference in the PCSA of this muscle group. The opposite was found in the wrist extensors, where the adult orangutan had much longer fascicle lengths than the juvenile orangutans, although again there was no difference in PCSA. While these particular differences may be attributed to ontogeny, the shoulder adductors and digital flexors of the chimpanzee Ptsm were found to have larger PCSAs than the other chimpanzees, even though all subjects, bar Chimp 95, were adult.

Substantial intra-individual differences were also found for the one subject (Ptsm) for which we were able to obtain measurements from both the left and right limb. In particular, the mean fascicle length of the elbow flexors was 36% longer in the left limb and the PCSA was 44% higher in the right limb; the elbow flexor group of the right limb was 12% heavier than the left limb, and the right limb also had a substantially greater PCSA than the left for the wrist flexors and digital extensors. In contrast, PtsmL had a substantially larger PCSA than all other individuals, including the right side of Ptsm, for the pronator group.

3.3.3 GLM analysis

Table 3.6 shows the results obtained from the GLM models for muscle belly mass, fascicle length and PCSA comparisons between the different species. For all belly mass models and the majority of fascicle length and PCSA models, only body mass was found to have a significant effect on the variation observed; neither species nor the interaction species*body mass were found to be significant. For fascicle length the exceptions were the pronators and wrist extensors. For the pronators, the main effect species resulted in a significant model but body mass did not (although it remained in the model as body mass was a covariate). Tukey's post-hoc test revealed that bonobos had significantly shorter pronator fascicles than both chimpanzees and gorillas, but they did not differ significantly from orangutans (Fig. 3.3a). For the wrist extensors, body mass alone was significant, but this significance was only achieved, together with a better fitting model, when species was also included, although the species effect itself was non-significant ($p = 0.072$). As species was necessary to produce the best fitting model for the wrist extensors Tukey's post-hoc test was performed. While no species were found to be significantly different, Figure 3.3b suggests that gorillas tend to have the shortest fascicle lengths in the wrist extensors, whereas chimpanzees tend to have the longest.

Table 4. Results from GLM models for forelimb muscle groups

Muscle group	Muscle belly mass			Muscle fascicle length			Muscle PCSA		
	$F_{\text{degrees of freedom}}$	R^2	p	$F_{\text{degrees of freedom}}$	R^2	p	$F_{\text{degrees of freedom}}$	R^2	p
Proximal muscles									
Shoulder adductors	$104.01_{1,12}$	0.90	<0.001	$13.05_{1,11}$	0.52	0.005	S: $5.97_{3,12}$	0.92	0.042
							B: $17.52_{1,12}$	0.92	0.009
							I: $594_{3,12}$	0.92	0.042
Shoulder flexors	$72.03_{1,13}$	0.85	<0.001	8.441,13	0.36	0.013	$25.65_{1,13}$	0.65	<0.001
Elbow flexors	$57.97_{1,14}$	0.80	<0.001	$7.33_{1,14}$	0.31	0.018	$15.62_{1,14}$	0.51	0.002
Elbow extensors	$369.46_{1,14}$	0.96	<0.001	$36.40_{1,14}$	0.72	<0.001	$72.66_{1,14}$	0.84	<0.001
Distal muscles									
Supinators	$32.44_{1,12}$	0.72	<0.001	$12.93_{1,11}$	0.52	0.005	$15.25_{1,11}$	0.56	0.003
Pronators	$149.27_{1,14}$	0.91	<0.001	S[1]: $6.79_{3,14}$	0.60	0.009	$51.38_{1,14}$	0.78	<0.001
				B: $3.07_{1,14}$	0.60	0.111[2]			
Wrist flexors	$54.75_{1,14}$	0.79	<0.001	$2.96_{1,14}$	0.12	0.109	$24.61_{1,14}$	0.63	<0.001
Wrist extensors	$154.76_{1,14}$	0.92	<0.001	S: $3.18_{3,14}$	0.38	0.072[2]	S: $446_{3,14}$	0.87	0.047
				B: $6.19_{1,14}$	0.38	0.032	B: $908_{1,14}$	0.87	0.020
							I: $438_{3,14}$	0.87	0.049
Digital flexors	$121.43_{1,14}$	0.90	<0.001	$4.37_{1,14}$	0.19	0.057	$24.39_{1,14}$	0.63	<0.001
Digital extensors	$142.5_{1,14}$	0.91	<0.001	$6.21_{1,14}$	0.27	0.027	$37.27_{1,14}$	0.72	<0.001

[1]In instances whereby body mass alone had a significant effect, this result is presented, in models whereby significance was obtained including both body mass (B) and species (S) as main effects, or the interaction species*body mass (I), the separate results are labelled accordingly. Due to insufficient data models are not presented for the shoulder rotators, shoulder abductors or shoulder extensors.

[2]Non-signficant results are presented in these two models as in the case of the pronators, body mass needs to be included in the model to take the effects of body mass into account. In the case of the wrist extensors although species was not significant, this was the best fitting model, and the only model whereby the result for body mass was significant.

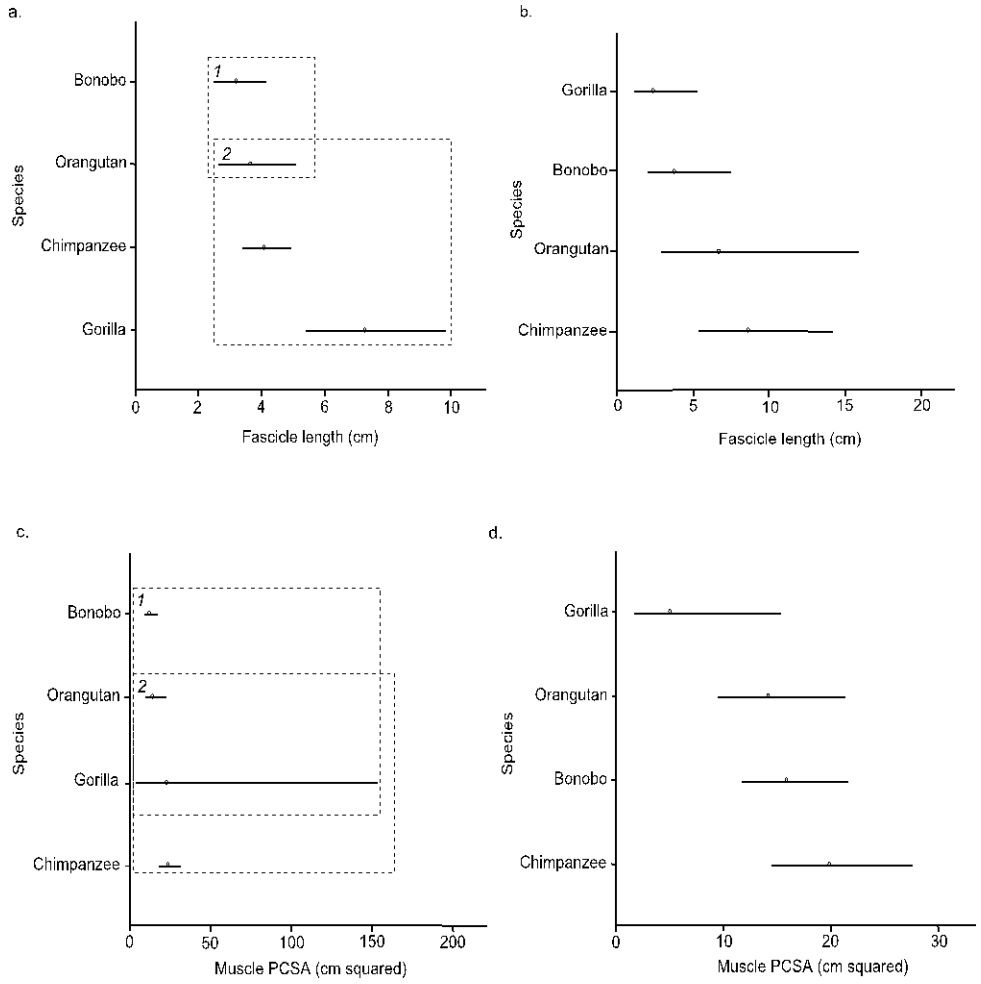

Fig. 3.3. Results from Tukey's post-hoc tests displaying mean values and 95% confidence intervals for the different species for a. pronator fascicle length; b. wrist extensor fascicle length; c. Shoulder adductor PCSA; d. wrist extensor PCSA. Values presented are back-transformed from logged data. Dashed boxes represent the significantly different sub-sets as highlighted from Tukeys post-hoc tests, if there are no dashed boxes Tukey's post-hoc did not reveal a significant difference between a specific pair.

For PCSA, the only models for which body mass was not the single significant effect were that for the shoulder adductors and wrist extensors where the model including both main effects (body mass and species) and the interaction, species*body mass, produced the most

significant result. Nevertheless, body mass had the most significant effect in both cases. Tukey's post-hoc tests revealed that the bonobos had significantly smaller shoulder adductor PCSAs than the chimpanzees ($p = 0.0460$; see Fig. 3c), whereas orangutans and gorillas did not differ significantly from either chimpanzees or bonobos. For the wrist extensors however, Tukey's post-hoc test revealed no specific difference between any pair of species (Fig. 3d). Nevertheless, it would appear that, as for fascicle length, the gorillas and chimpanzees were the most different, with gorillas having the smallest wrist extensor PCSAs of all species measured (Fig. 3d).

3.4 Discussion

3.4.1 Data collection and method of analysis

Previously, there has been an extensive study of forelimb anatomy in gibbons (Michilsens et al., 2009), and data are available for a number of chimpanzees and orangutans (Thorpe et al., 1999; Carlson, 2006, Oishi et al., 2008, 2009).To our knowledge, however, gorilla and bonobo forelimb muscle architecture data has not been published to date and an overall comparison of the forelimb musculature of the apes has not been undertaken. Our study therefore provides the first comprehensive overview of the variation in forelimb muscle architecture across the non-human apes.

An in-depth discussion of the different methods available for comparing anatomical parameters is presented in a previous paper (chapter 2). Allometric scaling using exponents from the data in question was found to be more appropriate than the use of geometric scaling

(as has been employed elsewhere, e.g. Thorpe et al, 1999; Payne et al., 2006; Oishi et al., 2009) because the data plotted as a line which did not fall through the origin (see Tanner, 1949; Schmidt-Nielsen, 1984; Packard and Boardman, 1999).However, as some studies have questioned any use of ratios for data comparison (e.g. Packard and Boardman, 1999). GLMs were also employed as a more appropriate technique by which to establish significant species differences, although the method ideally requires a reasonable sample size (chapter 2). In this study, although the sample size was much larger than has been possible in the study of great ape anatomy to date, our sample is still relatively small and further constitutes a range of age-sex classes. Thus to explore our dataset, analyses were undertaken using both allometric scaling and general linear models. The allometric scaling exponents obtained were similar to those found for primate hindlimb muscles (see Alexander, 1981; Pollock and Shadwick, 1994; chapter 2). For example in chapter 2 it was found that muscle mass scaled to a mean of $M^{0.84}$ (range $M^{0.53}$-$M^{1.27}$); fascicle length to $M^{0.15}$ (range $M^{-.0.04}$-$M^{0.31}$) and PCSA to $M^{0.70}$ ($M^{0.52}$-$M^{0.97}$). One would expect scaling exponents to be similar in the fore and hind limbs of quadrupedal animals which use both their forelimbs and hindlimbs equally. However, as discussed previously, when quadrupedal, primates such as chimpanzees tend to rely on their hindlimbs for propulsion and even steering and the forelimb tends to act just as a prop (see Li et al., 2004). However, as the apes as a whole are considered adapted for forelimb propelled behaviours e.g. climbing and suspensory locomotion, one might expect the forelimbs to scale with greater exponents than the hindlimbs, as was found with relative forelimb length in 'climbing' primates (see Jungers, 1984). Therefore, the similarity between the fore and hind limbs may reflect the range of behaviours performed by the non-human apes which involve use of both the forelimbs and hindlimbs during locomotion (e.g. Cant, 1987; Hunt, 1992; Doran, 1993a,b; Remis, 1995; Fleagle, 1999; Thorpe and Crompton, 2005, 2006).

3.4.2 Descriptive anatomy

One of the most significant variations in this study was the presence of a mono-articular long head in the biceps brachii muscle of orangutan Oaf, rather than the bi-articular arrangement that is normally observed (e.g. Swindler and Wood, 1973). No such observation was described by Sonntag (1924) or Oishi et al. (2008, 2009), although Oishi et al. (2008, 2009) presented only a small amount of descriptive data. A similar, but opposite, situation has been observed in gibbons, whereby the short head was monoarticular, originating from the lesser tubercle of the humerus, with the long head originating from the supraglenoid as normal (Michilsens et al., 2009). This was not observed in the gibbon (Hlf) in the present study. Reducing the ability of both heads of the biceps to act at the shoulder joint possibly reduces the flexion force capability at this joint. However, it is possible that this reduction in shoulder flexion is offset by an increase in elbow flexion, due to the increased leverage caused by an enlarged insertion which in the non-human apes extends more proximally on the humerus, enhancing the lever arm of these muscles (see Aiello and Dean, 2002), as has been proposed for gibbons (Jungers and Stern, 1980; Michilsens et al., 2009). Increasing elbow flexion force is likely to be beneficial for behaviours where body mass is suspended below a branch with the shoulder fully extended and the body is hoisted up by flexion of the elbow. Such behaviours are regularly used by both gibbons and orangutans, particularly during arboreal foraging and climbing (Fleagle, 1999; Isler, 2005; Thorpe and Crompton, 2005, 2006).

The presence of a separate flexor pollicis longus muscle with a tendon to digit one has not been commonly reported in the non-human apes, except in gibbons (see Aziz and Dunlap, 1986), but here it was observed in individuals Ppam, Gam and Oaf. A separate belly was also

observed in PtsmR and Gsm, although the tendon of insertion was to digit two, not one. A separate pollical flexor enables separate neuromuscular control of thumb flexion, enabling a precision grip (Aiello and Dean, 2002). Even though the non-human apes have a much smaller thumb than humans, the ability to perform a precision grip (whereby both small and large objects can be gripped; see Aiello and Dean, 2002) would be particularly useful during behaviours such as tool use and food manipulation The presence of a separate belly in some but not all individuals reflects individual variation and possibly also demonstrates an evolutionary tendency towards more specialised control of digital movements in hominoids.

3.4.3 Intra-specific variation

Differences between the right and left sides of the same chimpanzee (Ptsm) were apparent in a number of muscle groups from the allometrically scaled data. This may be due to the different positions of the limbs when the cadaver originally went into rigor before freezing, which may impact upon the fibre lengths and result in the differences observed. Specimen Ptsm was not frozen in the anatomical position and was an older specimen; this difference due to position was less of a concern for the other specimens which were frozen in the anatomical position. However, differences in limb usage may also account for the variation. The elbow flexors, in particular, had a much greater force producing capability in the right limb (PCSA was 43.98 % greater) and the PCSA in the wrist flexors and digital extensors was also greater in the right limb. These differences may reflect a need for laterality during important arboreal behaviours such as vertical climbing or for gripping and tool use, and laterality has been observed previously in the great apes (e.g. McGrew and Marchant, 1997; Peters et al., 2008). A similar arrangement was also observed in the key muscles involved in vertical climbing in the

hindlimb (chapter 2) and this increased ability to produce force in the limbs on one side of the body may reflect the use of a dominant side for propulsion and a non-dominant side for stabilisation as observed in humans during able-bodied walking (e.g. Sadeghi et al., 2000).

In general, there was a large amount of intra-specific variation, which is likely to be due to differences in age-sex class, the nature of the captive environments in which the animals had been housed, and individual variation. If different environments encourage more activity in some individuals and less in others this may explain the high level of variation seen, as in humans increased amount of inactivity results in a decrease in muscle volume and PCSA (e.g. Kawakami et al., 2000). This may explain the variation observed in the gorillas in particular as one would expect them to be more similar as they were all of the same age-sex class, except for Gsm. The gorilla Gsm was from the same enclosure as Gam, but Gsm was a sub-adult male. This age difference, therefore, may have resulted in different levels of activity between the two individuals. Age-sex differences were also evident in the orangutans, in particular, the increased force producing potential (larger scaled PCSA) in the juvenile orangutan's elbow flexors compared to the adult orangutan, relative to body mass. This may reflect the more explorative nature of juvenile orangutans and their increased use of arboreal climbing behaviours in both captive and wild environments (Thorpe and Crompton, 2005, 2006; Thorpe et al., 2009; Hanson et al., in prep).

3.4.4 Inter-specific variation

In all species the proximal muscles had the greatest PCSAs, in particular the shoulder rotators and shoulder extensors. The inclusion of latissimus dorsi, an extremely large back muscle, in

these groups, is likely the reason for their increased mass and PCSA. Latissimus dorsi is active during the support phase of vertical climbing and brachiation (Fleagle et al., 1981; Bogduk et al., 1998). Vertical climbing in particular is an important component of the locomotion of all the great apes, accounting for between 6.5% and 50.4% (Hunt, 2004) of their locomotor behaviour (Hunt, 1992; Doran, 1993a and b; Remis, 1995; Thorpe and Crompton, 2005, 2006). However, as pectoralis major was missing from the shoulder rotators, adductors and flexors, the PCSA of the rotators may have actually been much larger than any other group, and the remaining shoulder muscles may have been more equal. Fascicle lengths were also generally longer in the proximal muscles, particularly the elbow flexors and shoulder rotators, which together suggest the need for high forces to be exerted over a wide range of mobility at the shoulder and elbow, particularly during arboreal suspensory and climbing behaviours (Isler, 2005).

For all species measured here, the digital flexors had both the longest fascicles and the greatest PCSAs in the distal muscles. The importance of this muscle group in non-human great apes was to be expected as it enables greater grip strength. Grip strength is important when moving in an arboreal environment and it also enables fine manipulation of objects, necessary for tool use and dexterity when feeding e.g. ant dipping in chimpanzees (McGrew et al., 2005), leaf rolling in gorillas (Sawyer and Robbins, 2009) and seed and insect extraction in orangutans (Fox et al., 2004) . This situation contrasts with the case in cursorial species, such as dogs and horses, where the digital flexors usually have shorter fascicles and larger PCSAs, resulting in a reduced range of motion (e.g. Payne et al., 2005). In quadrupeds which are fore and hindlimb driven (e.g. dogs), however, this muscle architecture is necessary to enable them to cope with the greater proportion of vertical force that they experience

beneath the forelimbs (e.g. Li et al., 2004). Oishi et al. (2009) observed that their orangutans had longer fascicles and smaller PCSAs in their digital flexors compared to chimpanzees. In this study only chimpanzee (Ptsm) appeared to follow this pattern (from the scaled data), whereas all other chimpanzees were more similar to the orangutans and no differences were highlighted in the general linear model. Oishi et al (2009) speculated that this difference was likely due to the increased need for mobility in the wrist joint during arboreal behaviours in orangutans, and a greater emphasis on power in the chimpanzees during quadrupedal locomotion. Although this seems a reasonable conclusion, the discrepancy with our study highlights the differences which individual variation can make and demonstrates further the need to continue increasing the dataset of ape muscle architecture to enable more definite conclusions to be reached.

The intra-specific differences in this study made it difficult to visually assess if, and where, specific species differences were present, from the scaled data. A significant species effect was highlighted from the GLM models for PCSA in the wrist extensors, the chimpanzees having the greatest PCSA, and thus force production potential, and the gorillas the lowest. We suggest that that this variation may be related to a higher use of arboreal quadrupedalism by chimpanzees and bonobos compared to gorillas (Hunt, 1992; Doran, 1993a, b) and to associated differences in the kiniesiology of knuckle-walking between chimpanzees and gorillas as proposed by Kivell and Schmidt (2007). Gorillas use knucklewalking primarily in a terrestrial context, and are therefore able to maintain an inherently more stable columnar forelimb posture whereas the requirements of arboreal quadrupedalism, both transversely palmigrade and knucklewalking, in chimpanzees and bonobos lead to more flexed, and inherently less stable, elbow and wrist postures. Transversely palmigrade arboreal

quadrupedalism (placing the palm on the support with the hands turned out) requires greater force production in the wrist compared to the terrestrial knuckle-walking employed more frequently in gorillas, where the extensors are relatively inactive (Tuttle et al., 1972). As reportedly the most terrestrial of the apes, gorillas will climb into trees to feed, but rarely travel laterally between crowns (Remis, 1995; Ankel-Simons, 2000), thus reducing their need for force production during palmigrady, and mobility in their wrist extensors. Another factor contributing to higher PCSAs in the wrist extensors of bonobos and chimpanzees may be the role of this muscle group in synergic stabilisation of the wrist to allow the digital extensors and flexors to manipulate objects. This would be important during tool use, such as ant dipping, most commonly observed in chimpanzees and bonobos (e.g. McGrew et al., 2005).

Another observation apparent from the GLM, but not immediately apparent from the scaled data, was a significant difference between the PCSA of the shoulder adductors in the chimpanzees and bonobos. As bonobos had smaller PCSAs than the chimpanzees, this may reflect their ability to produce moderate forces over a greater range of motion (as the requirements of high force production are incompatible with high mobility). Bonobos are more arboreal than chimpanzees and perform vertical climbing substantially more (chimpanzees: 6.5% and bonobos: 50.4%; Hunt, 2004). One or both of these might create a greater need for mobility than for increased force potential. However, when comparing the allometrically scaled data it can be seen that the results from chimpanzee Ptsm may be disproportionately contributing to an apparent species difference as chimpanzees 94 and 95 and the bonobos are more similar. This was also the case with pronator fascicle length, as at least one of the chimpanzees was similar to the bonobos, even though the GLM found the

species to be significantly different. This again reinforces the need to be cautious when interpreting results from small sample size.

Any expectation for the greater behavioural arboreality, and putatively more frequent suspensory activity of the Asian apes, or even differences in kinematics of vertical climbing, between African and Asian apes to be accompanied by clear and unambiguous distinctions in forelimb muscle architecture from the non-human African apes is unsupported by this study. However, within the African apes degree of arboreality may have contributed to differences between panins and gorillines. Rather, it appears that behaviours which are selectively important will require adequate, but not necessarily more than adequate (Alexander et al, 1981) functional adaptations of forelimb musculature. Therefore the complete repertoire of behaviours performed seems to set the muscle architecture observed: and in the apes this is characterised by torso-orthograde behaviour, whether compressive or suspensory (Thorpe and Crompton, 2006; Crompton et al., 2008). However, adaptations to the frequencies to which different behaviours are performed, or relied upon, may well be reflected in muscle micro-architecture (i.e. different fibre type proportions), and it may be this which fine tunes muscles to the output required by a given species, or different populations of the same species (chapter 4). It is thus a knowledge of both macro- and micro-architecture that is required to appreciate the more subtle links between form, function and performances in the non-human apes (humans show a clear distinction from other apes in the greater power capacity of the hindlimb muscles (Thorpe et al . 1999).

3.4.5 Concluding remarks

This study contributes to the description of forelimb anatomy and muscle architecture in non-human apes, and in particular provides the first data on gorilla and bonobo forelimb muscle architecture. Overall we found that the non-human apes do not vary greatly in the forelimb across different physiological variables at the macro-level, reflecting that the Hominoidea as a whole are characterized by adaptation for a orthograde behaviours (Thorpe and Crompton, 2006) and that they share a close evolutionary history (Crompton et al., 2008). However, this study highlights the difficulty of comparing different species across only small sample sizes. With only small sample sizes, substantial variation between individuals (in for example, handedness) may swamp the signal of even real interspecific distinctions. Caution must be taken when drawing conclusions, as methods used to scale or analyse the data may exert untoward influence on results. It is imperative that more studies are carried out, preferably with fresh cadavers and utilising the same or at least directly comparable methods to increase sample size.

CHAPTER 4

DISTRIBUTION PATTERNS OF FIBRE TYPES IN THE TRICEPS SURAE MUSCLE GROUP OF CHIMPANZEES AND ORANGUTANS

Julia P. Myatt, Schilling, N. And Thorpe, S.K.S

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Different locomotor and postural demands are met partly due to the varying properties and proportions of the muscle fibre types within the skeletal muscles. Such data are therefore important in understanding the subtle relationships between morphology, function and behaviour. This is particularly useful when studying our closest living relatives, the great apes, as in the absence of soft-tissue characteristics from fossil data, they can aid in the reconstruction of ancestral locomotor patterns. The aim of this study was to determine the proportions of type I (slow) and type II (fast) fibres throughout the triceps surae muscle in chimpanzees and orangutans using immunohistochemistry. The orangutan had a higher proportion of type I fibres in all muscles compared to the chimpanzees, related to their slower, more controlled movements in their predominantly arboreal habitat. The higher proportion of type II fibres in the chimpanzees likely reflects a compromise between their need for controlled mobility in an arboreal habitat and their need for greater speed and power when terrestrial. There was no variation along the superficial to deep axis in either species, but there was some evidence of proximal to distal and medial to lateral variations in some muscles. Overall, this study has shown that not only do orangutans and chimpanzees have very different muscle fibre populations that reflect their locomotor repertoires, but it also shows how fibre type proportions provide an additional mechanism by which the performance of a muscle can be modulated to suit the needs of a species.

JPM conducted the data collection; analysed the data and wrote the manuscript. NS assisted with the data collection and the writing of the manuscript. SKST assisted with the writing of the manuscript.

4.1 Introduction

Different locomotor and postural demands are met, partly due to variations in gross anatomy (e.g. muscles present, points of origin and insertion, fibre lengths, pennation angles and physiological cross-sectional areas) (see Close, 1972; Alexander and Vernon, 1975) and partly due to variations in the physiological properties of the individual muscle fibres (reviewed by Pette and Staron, 1990) in the musculoskeletal system. Sarcomeres are the smallest functional units of muscles, containing the two proteins, actin and myosin, among others, that interact to enable a muscle to contract. The speed of muscle fibre contraction is largely determined by the myosin heavy chain isoform (MHC), leading to the distinction of two fibre types: fast and slow. Further analysis of the fibre's metabolic pathway based on myosin ATPase histochemistry reveals two types of pathway, either aerobic/oxidative or anaerobic/glycolytic. Combining these properties results in muscle fibres being defined as either fast (type IIa and IIb), also known as FOG (fast oxidative glycolytic) and FG (fast glycolytic) fibres respectively or slow (type I), also known as SO (slow oxidative) fibres. Further subtypes have been identified (see Punkt, 2002), but functionally, the distinction of fast and slow is best defined (Punkt, 2002). Type I fibres are fatigue-resistant and slow-contracting, whereas type II fibres are more fatigable, but fast-contracting. The proportion of these two fibre types throughout a muscle belly, in combination with different macro-architecture influences the function of a muscle.

While gross muscle architecture can be used to estimate functional properties such as force production and tendon stress (e.g. Thorpe et al., 1999; Payne et al., 2006, Channon et al., 2009), details of the fibre type distribution within muscles can provide further insight into the roles of different muscles and muscle regions, allowing more detailed relationships between

form and function to be established (e.g. Sickles and Pinkstaff, 1981a,b; Moritz et al., 2007; Schmidt and Schilling, 2007). For example, muscles with a high proportion of slow fibres tend to be predominantly used in anti-gravity, postural or endurance roles, whereas muscles with a high proportion of fast fibres are important for powerful, propulsive movements, such as jumping in addition to quick responses and counterbalancing movements, such as those needed during dynamic stabilisation (e.g. Sickles and Pinkstaff, 1981b; Rome et al., 1988; Schilling, 2009). In addition to a muscle having an overall proportion of fast and slow fibres, particular fibre types may be segregated into specific regions (reviewed by Kernell, 1998). Functionally, such fibre type regionalisation has been linked to the maintenance of joint stabilisation, energy-saving mechanisms and improving muscle efficiency (see Kernell, 1998; von Mering and Fischer, 1999).

Muscle physiology and gross architecture has been studied in some detail in non-human primates (for more recent examples see e.g. apes: Thorpe et al., 1999; Vereecke et al., 2005; Carlson, 2006; Payne et al., 2006; Oishi et al., 2008; Channon et al., 2009; Channon et al., 2010; Michilsens et al, 2010; other primates: Kikuchi, 2009), however, to date, we are not aware of any detailed study of the fibre type distribution in non-human ape hind-limb muscles, although Kimura (2002) has looked at the orangutan psoas major. The ability to relate form to function in non-human apes is crucial for developing our understanding of how subtle variations in morphology may relate to their positional behaviour repertoire. Furthermore, given the rarity of fossil hominoid data and the lack of information on soft-tissue characteristics, comparative studies of extant apes may be an important mechanism in the reconstruction of the locomotor repertoire of fossil hominoids.

The focus of this study was the triceps surae muscle group. This group is composed of two major muscles: superficially the gastrocnemius muscle with its two heads (lateralis and medialis), and lying deep to these, the soleus muscle. In both humans and non-human apes, the gastrocnemius muscle originates on the femur, whereas the soleus muscle originates on the tibia, with both inserting onto the calcaneus via the Achilles tendon. In addition to these two main muscles, the small plantaris muscle may be present, although it is absent in ~10% of humans, ~39% of chimpanzees and ~95% of orangutans (Langdon, 1990). The gastrocnemius muscle is biarticular, responsible for flexing the knee and plantarflexing the foot, whereas the soleus muscle only exerts a plantar-flexor moment about the ankle (Alexander and Vernon, 1975). The triceps surae muscles in chimpanzees and orangutans are characterised by long fibres and small physiological cross-sectional areas (PCSAs) when compared to humans, reflecting adaptations for relatively low force generation over a large range of joint displacements, beneficial for moving in an arboreal habitat (Thorpe et al., 1999; Payne et al., 2006). The triceps surae group of the non-human great apes is particularly interesting because, unlike humans, gibbons and most cursorial species, they have a substantially reduced external Achilles tendon (Swindler and Wood, 1973; Myatt pers. obs). Tendons function as mechanical energy stores during certain forms of locomotion, such as running, where they act as springs, returning energy with every step (Alexander, 1991, 1992). While we have long understood that the Achilles tendon plays a role in lowering the energetic cost of running in humans (Alexander, 1991, 1992), more recently, Maganaris and Paul (2002) have shown that it can also return energy during walking, albeit to a lesser extent. Muscle however has a major advantage over tendon in its ability to tune limb compliance to take account of changes in substrate properties such as irregularities, discontinuities and material characteristics, by active and controlled contraction, unlike tendon which is limited to passive extension (Roberts, 2002). The lack of an external Achilles tendon in non-human

great apes might suggest that adaptations for such control, which is particularly important for large-bodied arboreal primates, outweigh the benefits of energy return that would enable the use of jumping and running behaviours, as used by smaller primates in the same habitat. Whilst this makes sense for orangutans that are largely arboreal, chimpanzees move both terrestrially and arboreally, and when terrestrial undertake both fast dominance displays and long-distance patrols throughout their range (Goodall, 1990; Thorpe et al., 2002). This suggests that the requirement for faster, terrestrial locomotion should select for energetic efficiency i.e. a longer Achilles' tendon, but the arboreal requirements should limit the length of the Achilles' tendon in preference for muscular control. We would therefore predict that chimpanzees possess some form of compromise morphology at the micro-architecture level to aid in their terrestrial travel costs despite macro-adaptations for arboreality.

Fibre type proportion in various muscles of the triceps surae group have been studied in a range of species (e.g. human: Gollnick et al., 1974; Edgerton, 1975; cat: Burke et al., 1971; dog: Armstrong et al., 1982; cheetah: Williams et al., 1997) and under a range of conditions (e.g. bed-rest in humans: Ohira et al., 2000; spaceflight: Fitts et al., 2001; loading: Demirel et al., 1999; and aging: Deschenes, 2004). In general, these studies have found that most mammals have between 70 and 100% type I fibres in their soleus muscle e.g. cat (100%), rat (84%), guinea pig (100%), bush baby (87%) and slow loris (72%) (Ariano et al., 1973); long-tailed macaque (~94%) (Acosta and Roy, 1987). On average the gastrocnemius muscle has between 4 and 51% type I fibres e.g. rat (4%); cat (25%) (Ariano et al, 1973); cheetah (~40%); dog (~ 50%) (Armstrong et al, 1982); long-tailed macaque (~23%) (Acosta and Roy, 1987). As in other mammals, human studies have found that the soleus muscle contains the highest proportion of type I fibres in this muscle group, on average, between 70 to 80% type I

fibres, compared to the gastrocnemius muscle which contains between 57 and 64% type I fibres (Edstrom and Nystrom, 1969; Gollnick, 1974; Edgerton, 1975; Dahmane et al., 2005). The high proportion of type I fibres in the soleus muscle reflects the functional partitioning of this synergistic muscle group, resulting in the deeper, soleus muscle taking on the postural role during activities and slow locomotion, and the more superficial gastrocnemius muscle producing the propulsive forces for rapid and powerful ankle extension (see Smith et al., 1977; Walmsley et al., 1978; Spector et al., 1980). We would therefore anticipate both chimpanzees and orangutans to have a high proportion of type I fibres in their soleus muscle, as in other mammals. We further anticipate that orangutans will have a higher proportion of type I fibres throughout the triceps surae group because orangutans are predominantly arboreal, with their locomotion characterised by slow, cautious predominantly orthograde (upright-trunked) behaviours (Thorpe and Crompton, 2005, 2006; Crompton et al., 2008). In contrast, the locomotor behaviour of chimpanzees includes more powerful, swift movements, dominated by terrestrial quadrupedalism (Goodall, 1990; Hunt et al., 1992a, b), which is likely to result in a higher proportion of type II fibres in the gastrocnemius. Further investigation at the microscopic level (i.e. muscle fibre typing) may reveal in more detail how these animals meet the differing functional demands in their daily repertoire. The aim of the present study, therefore, was to determine the proportion and distribution patterns of type I and type II fibre types in the triceps surae group at five levels along the proximo-distal axis in chimpanzees and orangutans, using immunohistochemistry. Our goal was to contribute further to our understanding of how the musculoskeletal system of apes has adapted in the face of changing functional demands.

4.2 Material and methods

4.2.1 Specimens and sample preparation

Fibre type distribution was studied in two chimpanzees (*Pan troglodytes:* Blumenback, 1799) and one orangutan (*Pongo abelii:* Lesson, 1827) (see Table 4.1 for subject information), obtained after death in European zoos. All animals had no known musculo-skeletal problems and were considered healthy, active individuals prior to death. Animals were eviscerated during post-mortem examination and frozen for transport to Friedrich-Schiller-Universität Jena, Germany. The cadavers were then skinned and fixed in 4% formalin via immersion in a natural position. Once fixed, the triceps surae muscle group from the right leg was dissected out for further analysis.

Table 4.1. Subject information and gross muscle architecture

Subject	Sex	Age (years)	Mass (kg)	Cause of death	Obtained from:	Muscle	Muscle mass (g) (% of total body mass)[a]	Muscle length (cm) (% of body mass$^{1/3}$)[a]
Chimpanzee	Female	23	56	?	Belfast Zoo	S[b]	158.7 (0.3)	21.5 (56.2)
						GL and GM[c]	155.7 (0.3)	22.9 (59.9)
Chimpanzee	Male	34	62	Pulmonary embolism	Zoo Halle	S	190.3 (0.3)	24.5 (61.9)
						GL	120.3 (0.2)	28.2 (71.3)
						GM	96.7 (0.2)	21.8 (55.1)
Orangutan	Female	12	42	Drowning	Hamburg Zoo	S	63.8 (0.2)	16.9 (48.6)
						GL	40.4 (0.1)	16.3 (46.9)
						GM	77.2 (0.2)	19.0 (54.7)

[a] Following Alexander et al (1981).

[b] S: soleus; GL: gastrocnemius lateralis; GM: gastrocnemius medialis.

[c] Separate data for the gastrocnemius lateralis and gastrocnemius medialis muscles were not available for the female chimpanzee.

Muscles were removed from their points of origin to point of insertion, external tendons and facia were removed prior to the muscles being weighed and belly lengths measured (information provided in Table 4.1). The muscles were then frozen (-18°C) and divided into muscle blocks along the proximo-distal axis to obtain five equally distributed cross-sections along the length of the muscle belly (Fig 4.1). The number of blocks within each cross-section varied depending on the overall width of the muscle (up to 2 blocks), as they could be no larger than 3 cm by 3 cm for the histological processing. The gastrocnemius medialis and lateralis from both chimpanzees and the orangutan, and the orangutan soleus were simply divided into five overall cross-sections (e.g. Fig. 4.1a), whereas the chimpanzee soleus muscles were wider than 3 cm and therefore additionally divided proximo-distally into a medial and a lateral block resulting in 10 muscle blocks in total (e.g. Fig. 4.1b). Once the immunohistochemical labelling was performed on sections from the middle of each block, the overall muscle cross-section was re-assembled to visualise the distribution of muscle fibres across the complete cross-section and the five overall cross-sections were put together to analyse fibre proportion along the muscle's proximo-distal axis.

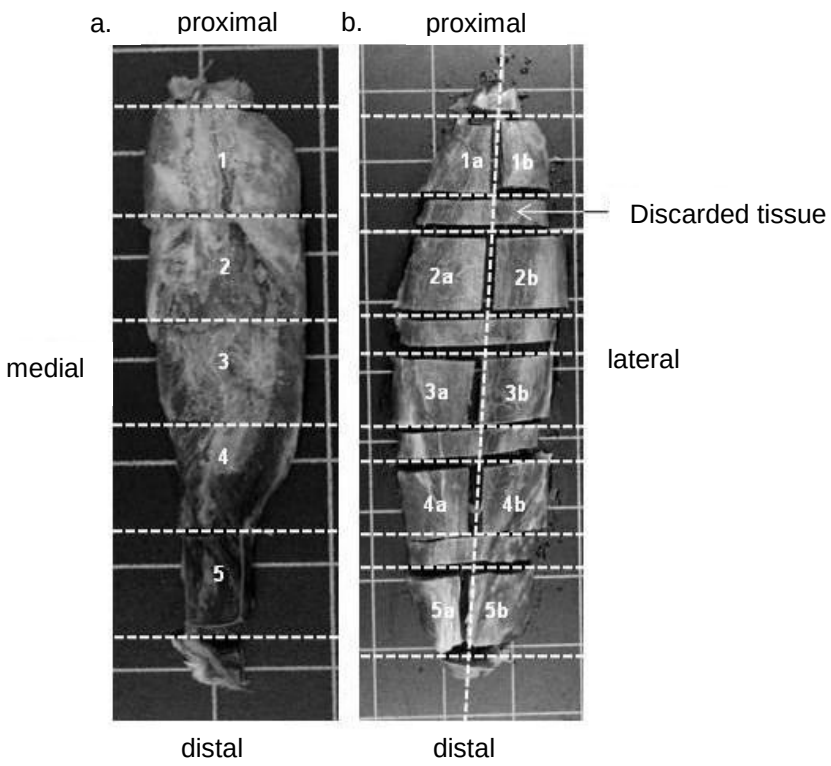

Figure. 4.1. Preparation of the muscle blocks for sampling the histological cross-sections from the five proximo-distal levels. Example of the A. orangutan soleus and B. female chimpanzee soleus (divided into two blocks at each level). Note that the investigated cross-sections were from the centre of each muscle block.

4.2.2 Immunohistochemistry

The muscle blocks were washed in distilled water and dehydrated with a graded series of ethanol (30%, 50%, 70% and 96%) and propanol over a period of 4 days, before being embedded in paraffin. Histological serial cross-sections were prepared (HM360 microtome, Microm, Germany; 10 µm) and several sections were sampled from the centre of each tissue block for immunohistochemical labelling.

Commercially available mouse monoclonal antibodies, raised against rabbit skeletal muscle, were used to identify fast-twitch (type II) and slow-twitch (type I) fibres (for detailed protocol see Schmidt and Schilling, 2007). To crosscheck fibre identification, enzyme histochemistry following Ziegan's protocol (Ziegan, 1979, modified after von Mering and Fischer, 1999) was additionally performed on a fresh sample from the male chimpanzee (Fig. 4.2). From this, we established that, firstly, type I fibres correlated with slow fibres, and type II fibres correlated with the fast fibres. Furthermore, among the type II fibres, type IIa fibres were present in the chimpanzee, in addition to other subtypes (Fig. 4.2). However, to identify the subtypes of type II fibres, fresh material frozen immediately after death is necessary, which is generally not possible with primate species or larger muscles, and therefore immunohistochemistry on fixed material was the only viable option, allowing us to identify type I and type II fibres only.

Initial testing on the fixed material for all three individuals found that the primary antibody to fast myosin (MHC II, Clone MY-32, Sigma-Aldrich Inc., Germany) produced both the greatest staining intensity and ease of distinction between the two fibre types, and was therefore used for all samples. In summary, the immunoreactivity of the muscle sample was first reinstated using trypsin (0.1%) in phosphate buffered saline (PBS, 0.01 M, pH 7.4), peroxidise activity was then blocked using 3% H_2O_2 in methanol before treating the cross-sections with normal goat serum (1.5% in PBS). The primary antibody was added and stained using a Mouse ExtrAvidin® Peroxidase staining kit (Sigma-Aldrich Inc., Germany), consisting of ExtrAvidin® Peroxidase and Biotinylated Purified Goat Antibody to Mouse IgG. To visualise the reaction, muscle samples were covered with a diaminobenzidine-H_2O_2 substrate. This stained the fibres containing the type II myosin heavy chain (type II fibres)

brown. Counterstaining was carried out using methylene blue (to contrast type I fibres), and slides were mounted with Euparal (Chroma, Germany), and cover-slipped.

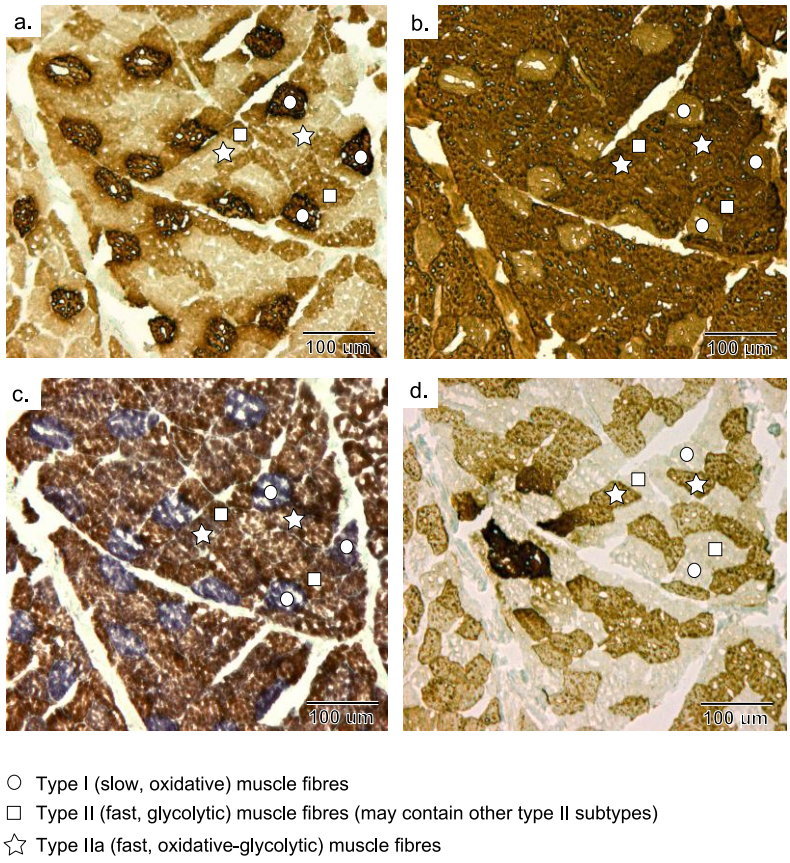

Figure. 4.2. Results of immuno- and enzyme-histochemical fibre identification in example of the male chimpanzee. A. anti-slow immune reaction. B. anti-fast immune reaction. Note the complementary staining result. C. Ziegan's enzyme reaction. D. anti-fast IIa immune reaction.

4.2.3 Quantification of fibre type distribution

To determine the distribution of type II (fast) and type I (slow) fibre types throughout the triceps surae muscle group, one of the serial histological sections collected from each tissue block was photographed using a digital camera mounted to a Zeiss® Axiolab microscope and analySIS® software (Soft Imaging System GmbH, Münster, Germany). Each section was approximately 3 cm by 3 cm or smaller, thus to identify and count individual muscle fibres,

multiple images were taken of each section in a systematic, grid-like pattern using the motor driven object table of the microscope. There was no overlap between adjacent photos.

To assess the percentage of fibre types within the muscles, the numbers of type I and type II fibres were counted in evenly spaced images based on a grid system and marked with the aid of ImageJ® to prevent double counting. Each image contained no more than 350 fibres, with the number of photos counted per muscle cross-section ranging from 30-155 depending on overall size. The proportion of each fibre type was then calculated as a percentage of all the fibres in a single image. In addition, the mean proportion of each fibre type was calculated for each cross-section. In the case of the chimpanzee soleus muscles the number of fibres from both the medial and lateral blocks were added together to obtain a mean proportion for the entire cross-section of the muscle at each proximo-distal level.

4.2.4 Statistical analysis

Mean percentages ± SE of type I and type II fibres for each cross-section and for whole muscles were calculated using SPSS v.15 (SPSS Inc., USA). To ascertain whether there were statistically significant differences between cross-sections within a muscle and at a given proximo-distal level between subjects, general linear models (GLMs) with binomial error distribution were conducted using the statistical package R v. 2.10.1 (www.R-project.org). All data conformed to the assumptions of normality. In cases where a statistically significant difference was established, Tukey's post-hoc testing was applied for all pair-wise comparisons, and in cases of variance heterogeneity (established by a Levene's test), a

sandwich estimator of the covariance matrix was additionally applied (Hothorn et al., 2008). Significance was taken at the $p<0.05$ level throughout.

4.3 Results

The percentages of type I and type II fibres for all subjects and their means are presented in Table 4.2. The two chimpanzees were found to differ in the mean proportion of type I fibres across the majority of comparable muscle cross-sections: the male chimpanzee had a significantly greater mean proportion of type I fibres in the soleus (52% compared to 41%; GLM: $F_{9,1850} = 70.29$, $p < 0.001$) and gastrocnemius lateralis (18% to 13%; GLM: $F_{9,1016} = 59.9$, $p < 0.001$) compared to the female chimpanzee. In contrast, there was a similar proportion of type I fibres in the gastrocnemius medialis of both chimpanzees, although there was again a significant overall difference between respective cross-sections (GLM: $F_{9,979} = 40.4$, $p < 0.001$). Within each chimpanzee, the two heads of the gastrocnemius muscle did not differ greatly in their proportion of type I fibres across equivalent cross-sections (e.g. gastrocnemius lateralis section one and gastrocnemius medialis section one in the female, Table 4.2). Results for the female chimpanzee only differed significantly between the lateral and medial heads across the second most proximal cross-section, with the gastrocnemius medialis having more type I fibres (Tukey: $p<0.01$). Results for the male chimpanzee differed significantly only across the second and fourth cross-sections, with the gastrocnemius lateralis having more type I fibres (Tukey: $p<0.001$).

Table 4.2. Percentages of type I and type II fibres from all muscles of the triceps surae group (values are mean percentages ± SE)

Muscle	**Soleus**		**Gastrocnemius Lateralis**		**Gastrocnemius Medialis**	
Muscle cross-section	**Type I fibres**	**Type II fibres**	**Type I fibres**	**Type II fibres**	**Type I fibres**	**Type II fibres**
Orangutan						
1 (proximal)	$87 \pm 1.5_{a,b*}$	13 ± 1.5	$31 \pm 1.7_{a,b,c*}$	69 ± 1.7	$47 \pm 1.5_{a,b,c*}$	49 ± 1.6
2	84 ± 1.7	16 ± 1.7	$37 \pm 1.0_{a}$	61 ± 1.4	$51 \pm 1.1_{a,d,e,f}$	47 ± 1.1
3	79 ± 1.7	18 ± 0.8	$36 \pm 1.4_{b,d}$	62 ± 1.6	$49 \pm 1.2_{d,g,h}$	50 ± 1.2
4	$68 \pm 1.2_{a,c}$	30 ± 1.0	$37 \pm 1.0_{c,e}$	63 ± 1.0	$41 \pm 0.9_{b,e,g}$	57 ± 1.0
5 (distal)	$64 \pm 1.2_{b,c}$	33 ± 1.0	$32 \pm 1.8_{d,e}$	63 ± 2.6	$34 \pm 2.5_{c,f,h}$	56 ± 3.4
Overall muscle	**72 ± 0.8**	**26 ±0.6**	**35 ± 0.6**	**63 ± 0.7**	**47 ± 0.6**	**51 ± 0.6**
Female chimpanzee						
1 (proximal)	$41 \pm 0.9_{h,i}$	58 ± 1.0	$12 \pm 0.5_{h,i,j}$	79 ± 2.2	$15 \pm 1.2_{h,i}$	85 ± 1.2
2	$39 \pm 0.8_{j,k,l}$	57 ± 1.0	$15 \pm 0.5_{h,k,l}$	80 ± 1.6	$17 \pm 0.5_{h,j,k,l}$	82 ± 0.9
3	$46 \pm 0.9_{h,j,m,n}$	52 ± 0.9	$15 \pm 0.5_{i,m,n}$	83 ± 1.2	$14 \pm 0.5_{i,j,m}$	78 ± 2.0
4	$41 \pm 0.9_{k,m,n}$	56 ± 1.0	$12 \pm 0.4_{j,k,m}$	88 ± 0.4	$11 \pm 0.6_{k,m,n}$	84 ± 1.9
5 (distal)	$36 \pm 1.0_{i,l,m,n}$	61 ± 1.2	$11 \pm 0.7_{l,n}$	84 ± 2.4	$14 \pm 1.1_{l,n}$	86 ± 1.1
Overall muscle	**41 ± 0.4**	**57 ± 0.5**	**13 ± 0.2**	**82 ± 0.8**	**14 ± 0.3**	**83 ± 0.8**
Male chimpanzee						
1 (proximal)	$50 \pm 1.1_{o,p}$	47 ± 1.1	$16 \pm 0.6_{o,p}$	82 ± 1.3	$17 \pm 0.6_{o,p}$	80 ± 1.5
2	$50 \pm 1.1_{q,r}$	45 ± 1.0	$21 \pm 0.5_{o,q,r,s}$	78 ± 0.9	$17 \pm 0.4_{q,r}$	81 ± 1.0
3	$49 \pm 1.4_{s}$	45 ± 1.4	$18 \pm 0.5_{q,t}$	82 ± 0.8	$16 \pm 0.5_{s,t}$	84 ± 0.7
4	$55 \pm 1.3_{o,q}$	43 ± 1.3	$17 \pm 0.7_{r,u}$	79 ± 1.7	$14 \pm 0.5_{o,q,s,u}$	83 ± 1.6
5 (distal)	$55 \pm 1.3_{p,r,s}$	40 ± 1.1	$11 \pm 2.0_{p,s,t,u}$	89 ± 2.0	$12 \pm 0.7_{p,r,t,u}$	86 ± 2.1
Overall muscle	**52 ± 0.6**	**44 ± 0.6**	**18 ± 0.3**	**81 ± 0.6**	**16 ± 0.2**	**82 ± 0.6**

*paired letters in subscript refer to a significant difference (p<0.05) in the percentage of type I fibres between the muscle-cross sections using Tukey's post-hoc test e.g. orangutan soleus section 1 is significantly different from section 4 (as indicated by letter $_{a}$).

Nevertheless, taken as a whole, the mean proportions of type I and type II fibres in the two chimpanzees were clearly more similar to each other than either were to those of the orangutan for all muscles. The orangutan had a much higher mean percentage of type I fibres across all muscle sections compared to both chimpanzees, with an overall mean of 72% type I fibres in the soleus compared to 41% and 52% in the female and male chimpanzees respectively. The overall mean proportion of type I fibres in the two heads of the gastrocnemius muscle varied slightly in the orangutan, with the medial head having a significantly higher percentage than the lateral head (47% and 35% respectively) (GLM: $_{F9,670}$ =59.48, p<0.001). When comparing equivalent cross-sections there was a significant difference between the proximal four sections, with gastrocnemius medialis having a higher proportion of type I fibres (Tukey: p<0.01), but there was no significant difference between the most distal cross-sections (Tukey: p = 0.569).

The proportion of fibre types differed significantly along the proximo-distal axis of the muscle for all muscles in both chimpanzees (female chimpanzee: soleus GLM: $F_{4,906}$ = 24.13, p<0.001; gastrocnemius medialis: $F_{4,452}$ = 51.02, p<0.001; gastrocnemius lateralis: GLM: $F_{4,525}$ = 40.59, p<0.001, male chimpanzee: soleus GLM: $F_{4,944}$ = 10.8, p<0.001; gastrocnemius medialis: GLM: $F_{4,527}$ = 13.22, p<0.001; gastrocnemius lateralis: GLM: $F_{4,491}$ = 59.61, p<0.001). Tukey's pairwise relationships (shown as paired subscript letters in Table 4.2) show that almost all cross sections within each muscle contributed to the overall significant difference (taken at the p<0.05 level). Overall, proximo-distal variation was also apparent in all orangutan muscles, with there being a significant difference between the majority of cross-sections (soleus GLM: $F_{4,428}$ = 79.05, p<0.001; gastrocnemius lateralis GLM: gastrocnemius lateralis: GLM: $F_{4,279}$ = 10.99, p<0.001; gastrocnemius medialis: GLM: $F_{4,391}$ = 61.2,

$p<0.001$; see Table 4.2 for Tukey's pairwise relationships across the cross-sections within each individual muscle).

However, the pattern of variation within all muscles of the triceps surae along the proximo-distal axis differed between the chimpanzees and the orangutan (Table 4.2; Appendix III). The male chimpanzee showed a slight increase in type I fibre proportion from 50% to 55% towards the distal end of the soleus muscle, but this was the opposite gradient to that observed in the orangutan where the number of type I fibres decreased significantly from 87% proximally to 64% distally. The female chimpanzee had a slight peak in proportion of type I fibres in the middle of the soleus muscle. The pattern of fibre proportion within gastrocnemius lateralis was similar in the chimpanzees in that the number of type I fibres slightly decreased towards the distal end of the muscle. The same was true for the male chimpanzee's gastrocnemius medialis. In the orangutan gastrocnemius lateralis there was a slight peak in type I fibres in the middle of the muscle belly, this was also the case in the orangutan and female chimpanzee's gastrocnemius medialis muscles.

Overall there was little variation along the superficial-deep and medio-lateral axes in all muscles (Appendix III), although some variation was apparent in the medio-lateral axis of the chimpanzee soleus muscles. In the female chimpanzee soleus there was a decrease in the proportion of type I fibres from ~50% on the medial side and in the centre of the muscle to ~20% along the lateral edge (Appendix IIId). The proportion of type I fibres in the male chimpanzee decreased from ~70 % on the medial side and in the centre of the muscle to ~30% in the lateral quarter (Appendix IIIg).

4.4 Discussion

4.4.1 Sample selection

The origins and insertions of all muscles in this study agreed with previous studies (Swindler and Wood, 1973; Thorpe et al., 1999; Payne et al., 2006a; Myatt, unpublished data), and the masses of muscles sampled in this study, and their percentage of total body mass, are similar to the range previously observed (Thorpe et al., 1999; Payne et al., 2006; Myatt, unpublished data), showing that this was a normal, healthy sample. Housing conditions of captive animals may influence fibre type populations compared to their wild counterparts due to factors such as support type and activity level. However, all of the individuals in this study were considered healthy, active individuals immediately prior to death and their captive conditions allowed for varied support use, mimicking that observed in the wild. Furthermore, Williams et al. (1997) found that the fibre type composition in wild cheetah compared to less active captive cheetah did not differ significantly; therefore, we consider the proportion of fibres observed in this study to be representative for chimpanzees and orangutans, although we acknowledge that a larger sample size would be beneficial.

4.4.2 Intra-specific comparison between chimpanzees

There was a significant difference in the absolute proportions of type I fibres between the cross sections of the triceps surae muscles of the two chimpanzees (mean difference: soleus 11%; gastrocnemius lateralis 5%; gastrocnemius medialis 2%) and this could be related to a range of factors, including genetic variability (e.g. Simoneau and Bouchard, 1995), sex (e.g. Deschenes, 2004), age (e.g. Deschenes, 2004), activity level (e.g. Monster et al., 1978) and

body size (Kram and Taylor, 1990; Seow and Ford, 1991). In this instance the observed difference in fibre proportion between the two chimpanzees is unlikely to be related to age as both chimpanzees were fully-grown adults. As the chimpanzees were different sexes we could expect that the difference in body mass may have had some effect (the male chimpanzee was 11% heavier than the female), as with increasing body mass there is usually an increase in the proportion of type I fibres to cope with the increasing forces necessary to support body weight against gravity (see Kram and Taylor, 1990; Seow and Ford, 1991). Unidentified genetic factors are also thought to account for up to 25% of the variability in fibre type distribution between individuals, with differences in behaviour and the level of muscular contractile activity accounting for 30% (Simoneau and Bouchard, 1995). Wild and captive male chimpanzees often carry out patrols of their territories, lasting a number of hours and covering distances as great as 35 km (Goodall, 1990; Watts and Mitani, 2001; Thorpe, pers. observ.). This may explain some of the greater type I proportion observed in the male's triceps surae muscle, as they would need more stamina, however, captive chimpanzees cover much smaller distances than their wild counterparts, more similar to females (Thorpe, pers. obs.), further supporting the idea that most of the variation between the two chimpanzees could be explained by genetic variation. The greatest mean difference between the two chimpanzees was 11%, therefore, theoretically, all of the variation could be accounted for by genetic variation (Simoneau and Bouchard, 1995); however, other factors should also be considered.

Variations along the different axes within the muscles of the triceps surae were similar between the chimpanzees. A slight increase in the proportion of type I fibres distally was apparent in the soleus muscle, although this was not as clear as the medial to lateral variation,

whereby the proportion of type I fibres decreased towards the medial side. This is in contrast to the homogeneity of the predominantly type I population usually observed in the soleus muscle of mammals (e.g. Ariano et al, 1973; Edgerton et al, 1975). During quadrupedal walking, at the beginning of stance, chimpanzees and bonobos place their foot down through the heel and lateral mid-foot, with the highest pressures experienced under the lateral mid-foot (Wunderlich and Ford, 2000; Vereecke, 2006). As they roll over onto the outside of their foot, this causes an outward rotation of the ankle which may be stabilised by the increased number of type I fibres on the lateral side of the soleus muscle.

4.4.3 Inter-specific comparison between chimpanzee, orangutan and other mammals

Although the two chimpanzees differed in their fibre type proportions, these differences were small in comparison to those between the chimpanzees together and the orangutan. The chimpanzees and orangutan were similar in that their soleus muscles had more type I fibres than either head of the gastrocnemius muscle, as is apparent in most mammals (e.g. Ariano et al., 1973; Edgerton et al., 1975). The greater proportion of type I fibres in the soleus is generally evident in all synergistic muscle groups whereby the deeper muscle consists predominantly of type I fibres and may reflect optimisation of the lever arm for different tasks (Kernell, 1998; Dickx et al., 2010). The orangutan, however, had a much larger proportion of type I fibres across all muscles. This agrees with our predictions since orangutans move much more slowly than chimpanzees, which requires slow, sustained contractions, as has also been observed in other, but rather slower, arboreal animals such as the slow loris (Sickles and Pinkstaff, 1981b) and sloth (Bárány et al., 1967).

Whilst it was anticipated that the chimpanzees would generally have a greater proportion of type II fibres compared to the orangutan, the proportion of type II fibres in their soleus muscles (female: 41%, male: 52%) was high compared to that in most mammals studied e.g. human: 20-30% type II fibres (Edstrom and Nystrom, 1969; Gollnick, 1974; Edgerton, 1975; Dahmane et al., 2005); long-tailed macaque: ~10 % type II fibres (Acosta and Roy, 1987) and cat (0%), rat (16%), guinea pig (0%), bush baby (13%) and slow loris (28%) (Ariano et al., 1973). An increase in the proportion of type II fibres in a postural muscle can result from an extreme lack of use (see Loughna et al., 1990; Jaenicke et al., 1991; Scott et al., 2001), but this is unlikely to be the case here as the chimpanzees were healthy, active individuals immediately prior to death. The higher proportions of type II fibres in the chimpanzee soleus muscle seem to suggest that this muscle plays a role in functions other than maintenance of posture. Type II fibres are able to produce force more rapidly than type I fibres, and may also have greater peak power output (see Walmsley et al, 1973; Bottinelli et al., 1996; Widrick et al., 1996). At a macroscopic level, force production can be increased by having shorter muscle fascicles and a larger PCSA, but this results in restricted joint mobility and velocity of shortening (Thorpe et al., 1999; Payne et al., 2006). An increase in type II fibres may thus be an important mechanism, by which chimpanzees facilitate increased power and acceleration when terrestrial despite their gross morphological adaptations (long muscle fascicles and smaller PCSAs) to the greater joint mobility required when moving in an arboreal habitat (Thorpe et al., 1999; Payne et al., 2006). Hindlimb power and acceleration will be important for chimpanzees during conflict and social interactions involving both sexes (Goodall, 1990) and during high-speed terrestrial travel.

In contrast to the chimpanzees, where both the medial and lateral gastrocnemius had a similar proportion of type I fibres, there was a greater difference in the proportion of type I fibres between the two heads of the gastrocnemius muscle in the orangutan. In the orangutan, the gastrocnemius lateralis had a greater proportion of type II fibres, possibly indicating that this muscle is more likely to be recruited at faster locomotor speeds, or used for dynamic stabilisation (Schilling, 2009). Increased ability to rapidly stabilise the ankle and lower limb on the lateral side may be more beneficial for orangutans during behaviours such as vertical climbing and bipedal scramble (where the torso is upright and most of the weight is borne by the hindlimbs, but supports are small, irregularly placed and angled: Thorpe and Crompton, 2006), where their hip and knee joints are more mobile and rotated outwards, and their ankle joint is more strongly inverted, in comparison to chimpanzees (Isler, 2005; DeSilva, 2009; Myatt, pers. observ.). During these extreme positions the stresses experienced on the lateral side would be higher and the ability to rapidly compensate for movements of the flexible, arboreal supports would be crucial, increasing the need for type II fibres on this side.

The orangutan also showed a clear proximal to distal gradient in the soleus muscle, with the proportion of type I fibres decreasing distally. This places more type II fibres at the distal end of the muscle belly, in close proximity to the Achilles tendon and its aponeurosis. At the muscle-tendon junction type II fibres have a greater surface area dedicated to force transmission than type I fibres (Trotter and Baca, 1987). Therefore, positioning the type II fibres closer to the tendon of insertion may enable more effective and immediate force transmission for dynamic stabilisation to compensate for sudden, unexpected movements in their constantly shifting environment. Furthermore, although orangutans do not have a significant Achilles tendon, aponeuroses are also able to store elastic energy, both along the

longitudinal and transverse axes, and their stiffness can be modulated depending on the type of contraction (Azizi and Roberts, 2009). This, along with the variable gearing mechanism of pennate muscles (Azizi et al., 2008) and the placement of different fibre types throughout the muscle belly, may reflect the ability of a muscle to adapt depending on the mechanical demands of a particular behaviour, although further study and in vivo analysis would be necessary to investigate the behaviour of this muscle-tendon unit in more detail.

The smaller length of the Achilles tendon in chimpanzees and orangutans, compared to humans and cursorial mammals, implies that they rely less on energy return from this tendon during their locomotion. Rather, they benefit in an arboreal habitat by having more muscle that is better able to cope with irregularities and flexibility in habitat structure, by controlling the level of contractile activity and being able to tune muscle contractions more precisely through variable placement of the muscle fibre types, rather than being limited to passive extension like tendon (Roberts, 2002). Chimpanzees and orangutans further benefit in an arboreal habitat by being able to produce moderate forces over a greater range of joint mobility; an adaptation which is reflected in the macro-architecture of their muscles (Thorpe and Crompton, 2006; Payne et al., 2006). However, by possessing longer muscle fibres and smaller PCSAs, in contrast to the situation in humans, chimpanzees and orangutans are limited in their ability to produce high forces. Unlike orangutans, chimpanzees undertake quadrupedal running in short bursts, requiring high accelerations and forces, and long distance patrols, behaviours which may benefit from an Achilles tendon to some extent. Adaptations to their arboreal habitat, however, possibly outweigh the advantages of an Achilles tendon. Chimpanzees, therefore, appear to have a greater proportion of type II fibres

throughout their triceps surae muscle relative to humans and orangutans, to enable them to perform those

behaviours requiring speed and power. The locomotor repertoire of orangutans, on the other hand, does not often include behaviours requiring more power or speed, resulting in a muscle fibre profile more similar to that of humans, who produce high forces by having large PCSAs. Orangutans are unable to produce the high forces because their adaptations to mobility limits the PCSA of their muscles and their need to maintain controlled contractions in their arboreal habitat increases the need for type I over type II fibres. Therefore, orangutans may be limited to slow locomotion by their muscle physiology, although the risky, fragile nature of their arboreal habitat also imposes its own restrictions.

4.4.4 Concluding Remarks

This study is a first step to providing insight into how the different great apes are adapted to their habitats and lifestyles at the micro-architecture level, although we acknowledge the limitations of the study with regards to sample size and the ability to discern between fast and slow fibre types only. Further studies, increasing both the number of individuals and species studied would be beneficial; gibbons, in particular, would be of interest as they combine a long Achilles tendon with an arboreal locomotor repertoire. Overall, this study has shown that not only do orangutans and chimpanzees have very different muscle fibre profiles that reflect their locomotor repertoires, but it also shows how adaptations in micro-architecture provide an additional parameter by which the output of a muscle can be modulated, and the

fine tuning of control is possible. Only by combining data from all aspects of muscle architecture can we truly appreciate the subtle links between form and function and increase our knowledge of the evolution of great ape locomotor repertoires.

CHAPTER 5

A NEW METHOD FOR RECORDING COMPLEX POSITIONAL BEHAVIOURS AND HABITAT INTERACTIONS IN PRIMATES.

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In an arboreal habitat, primates have to cope with many problems, such as multiple, flexible supports, in order to obtain food, find mates and avoid predators. To understand how animals interact with these complex environments we can study their positional behaviour. However, due to the intricate nature of locomotor and postural variation it can be difficult to capture the fine-grained details such as limb use (i.e. weight and balance), limb flexion and substrate use. In the present study, such a method was developed, based on the movement notation technique, Sutton Movement Writing. Our aim was to record the spatial arrangement of limbs during positional behaviours, and their use of multiple, compliant supports, that could be replicated for any primate species. The technique was validated and tested for inter- and intra-observer reliability using data from orangutans. Overall, Sutton Movement Writing shows considerable promise for increasing the resolution with which positional behaviours can be recorded under field conditions and provides a way to extract numerical data for use in statistical analyses. This will facilitate understanding of how behaviours and species vary in response to the environment, and the capabilities of primates to perform key tasks in their different niches.

JPM developed the method, carried out the data collection, analysed the data and wrote the manuscript. RHC assisted with method development and the writing of the manuscript. SKST also assisted with method development and the writing of the manuscript.

5.1 Introduction

An animal's biological success relies on its ability to move through its environment to find key resources such as food and mates, and to avoid predators (Cant, 1992). The study of positional behaviour (locomotion and posture) therefore provides important information about how animals solve problems associated with living in complex habitats. Our understanding of positional behaviour and associated morphology has been greatly enhanced by the use of standardized, pre-defined classification systems which group biomechanically similar positional behaviours together (for recent examples see: Thorpe and Crompton, 2005, 2006; Bitty and McGraw, 2007; Wright, 2007; Prates and Bicca-Marques, 2008, all of which build on the work of Hunt and colleagues', 1996 system). In such classification systems, behaviors are placed into one of a number of pre-determined modes, which can then be broken down into more distinct sub-modes (Hunt et al., 1996; Thorpe and Crompton, 2006).

While these methods provide a valuable overview of the observed postural and locomotor repertoire of a species, they are limited in their ability to record complex spatial arrangements of multiple limbs and multiple, compliant supports, such as occur during feeding on thin terminal branches, or mechanically complex behaviours such as tree sway in orangutans. Obtaining these finer details can enhance understanding of how species of similar mass and morphology, such as the apes, employ subtly different strategies to achieve the same goals (Gomberg et al, 1979; Bock & von Wahlert, 1998). Filming such behaviours may appear to be the answer to recording this increased level of complexity. Video cameras, however, are often of limited use in field situations, particularly when rare behaviours are of interest, as they are not easy to anticipate and data are often lost due to the time taken to set up the camera.

Furthermore, using a video camera throughout a field day, which can often last in excess of 12 hours is generally not feasible due to restrictions on camera battery life. In addition to these practical issues it can also be more difficult to ascertain heights, sizes, angles and three-dimensions from video, than when viewing the animal in real time.Therefore, the aim of this study was to identify a method that allows increased resolution of positional behaviours under field conditions, without relying on video cameras, to enable more specific questions about the solutions that animals adopt to survive in complex environments to be asked.

Such a method was found within the field of movement notation. Movement notation systems were originally developed to record forms of dance, particularly ballet (e.g. Eshkol-Wachmann movement notation [Eshkol and Wachmann, 1958]; Labanotation [Knust, 1959; Hutchinson, 1990, 1996]; Sutton Movement Writing [Sutton, 1981]). They have since been used to record aspects of positional behaviour, (e.g. sitting, Kember, 1976) and motor control (e.g.; Metz and Whishaw, 2000; Foroud et al., 2004; Vasey et al., 2006). Notation systems appear capable of accurate recreation of complex behaviours from large scale (whole body) positions to facial expressions (e.g. Causley, 1967; Sutton, 1981; Hutchinson, 1990, 1996) and can be adapted for use in a range of situations. Of these, Sutton Movement Writing (SMW) (Sutton, 1981) is the most suitable for studying positional behaviour in the field as it: enables a figure to be depicted faster and in a more pictorial manner than in other notation and classification systems (Sutton, 1981); enables real-time detailed recreation of postures and slow locomotion with little training; allows recording of additional features such as habitat variables; and can be employed using continuous, instantaneous or *ad libitum* sampling techniques. In this paper we introduce the method of SMW and test its efficiency using wild

Sumatran orangutans (*Pongo abelii*) as an example and describe situations where SMW may contribute to studies of primate positional behaviour.

5.2 Method

The traditional SMW approach (Sutton, 1981) of drawing a figure representing the subject using a 5-line stave was simplified into a free-body stick figure form, supplemented by additional symbols to provide contextual and habitat information (see Fig. 5.1 and Table 5.1). To increase the ease with which behaviours could be recorded in the field, when recording locomotion, movements were simply treated as a sequence of static postures.

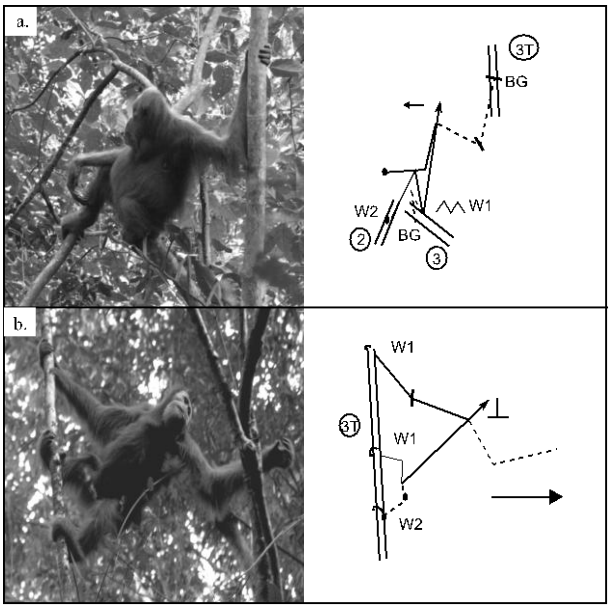
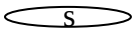
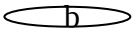


Fig. 5.1. Examples of postural (a) and locomotor behaviours (b, tree sway) on the left with their associated SMW figure diagrams on the right. For explanation of symbols used see Table 5.1 and for details see text.

Table 5.1.Symbols used to annotate SMW figures

Feature described	Meaning	Symbol
Body parts	Torso and head	
	Right-side limbs	
	Left-side limbs	
	Ischia	
	Stomach	
	Back	
	Hand/foot*	
Direction in which	Away from the observer	
the animal is facing	Toward the observer	
	To the right	
	To the left	
Three-dimensionality	In front of the coronal plane	
of limb positions	Behind the coronal plane	

*Hand/foot symbol is simply a curved line which can be drawn around the support as viewed if necessary to distinguish between different grips.

The animal's head was denoted by an arrow-head, with an adjacent symbol to indicate the direction it was facing (Fig. 5.1 and Table 5.1.). Body and limb positions were drawn as observed, with left and right limbs differentiated using solid and dashed lines respectively. If necessary the hand or foot grip could also be drawn; this was important in situations where depending on the position of the foot or hand, the limb could be bearing weight in either suspension or compression (see Fig. 5.1b for an example). The degree of limb flexion at the hip, knee, shoulder and elbow was drawn as either fully extended (range ~0 ^{o}- 30 ^{o}), slightly flexed (range ~30 ^{o}- 120 ^{o}) or tightly flexed (>120 ^{o}, e.g. knees close to the sides of the body as in *sit* or *squat*), to simplify the recording procedure whilst retaining a close functional reflection of the limb positions.

Additional abbreviations written next to the relevant limb (or body part) (see Fig 5.1 and Table 5.1) indicated an estimate of the proportion of weight borne by each (either W1: those bearing the majority of body weight or W2: those bearing more than their own weight, but less than main weight bearing parts). Limb loading was estimated from the degree to which supports deflected under the animal's mass, combined with the position and amount of tension in the limbs (following Hunt et al., 1996; Thorpe and Crompton, 2006). Limbs contacting a support, but not bearing more than their own weight, were assumed to contribute to balance or stability and were labelled as BG (balance grip) or BT (balance touch). For locomotion, a large arrow was drawn next to the figures to show the direction of travel.

To depict three-dimensionality of limb positions in a two-dimensional representation, limbs were defined as consisting of two segments, with each segment consisting of one fixed end (the proximal joint's centre of rotation e.g. the shoulder for the upper arm or elbow for the lower arm), and one free end (e.g. the elbow/wrist respectively). In addition, if required, further detail relating to the hand or foot position could be included if necessary. Following Eshkol and Wachmann (1958), if the fixed end was taken as the centre of a reference sphere, the relative orientation of the free end could be classified according to its position within the sphere in one of 26 pre-defined positions, situated 45^{o} apart (Fig. 5.2). This degree of precision is suitable for field studies, where the viewing distance and issues of parallax may result in any finer-grained estimates being inaccurate. To enable segments from SMW figures to be transferred into the sphere positions, a segment was illustrated as either anterior or posterior to the coronal plane using a circle or bar symbol respectively, placed across the relevant joint. Absence of a symbol indicated that the segment remained in the coronal plane (see Fig. 5.1 for examples and Fig 5.2. for further explanation). If the limb was fully extended

at the elbow or knee it was treated as a single segment. Regardless of the observers' actual viewpoint, figures could be drawn from a lateral or frontal perspective to make the positioning of limbs clearer.

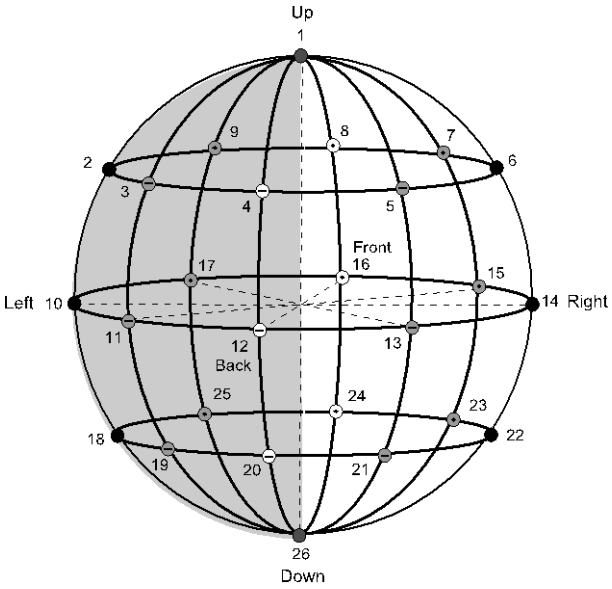


Fig. 5.2. System of reference used to quantify the positions of each limb segment, the head and additional body parts in space with divisions 45^{o} apart (Adapted from Eshkol and Wachmann, 1958). The 26 positions are labelled accordingly. Those marked with a circle in the centre are in front of the coronal plane, those with a line, behind the coronal plane. Unmarked positions are in-line with the coronal plane. SMW figures are best drawn from a lateral perspective when limbs are in positions shaded in white, and from a frontal perspective when limbs are in positions shaded grey or black, using a circle, line or no symbol as required, as this makes the postures easier to discern. The centre of the sphere may be defined either as the centre of the body in order to record the position of the head and other body parts, but may also be defined as the centre of rotation of individual limb joints to record the position of each segment. The sphere is placed with position 26 (down) parallel to the ground when recording head and body part positions, but parallel to the feet of the animal (as if standing bipedally) when recording joint segment positions. To remove laterality only half of the sphere (e.g. the half used to label right limbs) can be used to label all limb positions, except those crossing in front of the body which would use the other half of the sphere.

Arboreal supports used by the animal were drawn next to the limbs or body parts contacting them, with notation to indicate the support's type and diameter class (e.g. 3T in Fig. 5.1). Diameter classes were: 1: 0<2 cm; 2: ≥2<4 cm; 3: ≥4<10cm; 4: ≥10<20cm; 5: ≥20cm (after Cant, 1987) and support type classes were: T: tree trunk; B: boughs/ branches and L: liana. Additional details could also be recorded, such as contextual behaviour, distance travelled or measures of overall tree size, such as diameter at breast height and overall height, as needed.

5.2.1. Extraction of data from SMW

In order to extract data from SMW for meaningful analyses, the sphere of reference visualized around the figure to depict the three-dimensionality of limb positions (Fig 5.2; Eshkol and Wachmann, 1958) was used to provide a sequence of numbers related to the position of each segment that describes the overall posture. This resulted in a series of 8 numbers relating to the positions of the main limb segments (i.e. the upper and lower arms and upper and lower legs). Additionally, the positions of the head and ischia were incorporated to provide an overall sequence of 10 numbers. If laterality was of interest (e.g. Peters and Rogers, 2008), the whole sphere was used to identify the positions of the limbs on both sides of the body, but this process was simplified if the user does not need to distinguish between left and right limbs, by not using the grey shaded half of the sphere (unless a limbs crosses over in front of the body). For example, to describe a simple bipedal stand, as in Fig 5.3c, distinguishing between left and right sides of the body, both hindlimbs would be in position 26 (both segments), the right forelimb (both segments) would be in position 22, with the left upper arm segment in position 10 and the lower left arm segment in position 6 (as it is crossing back across the body), the head would be in position 1.

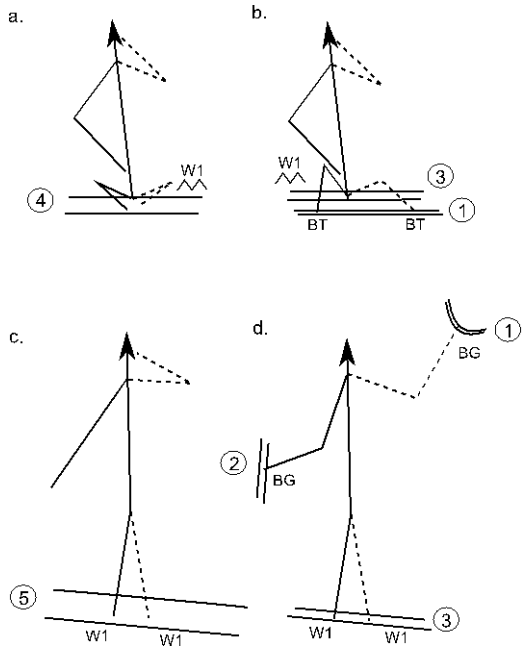


Fig 5.3. Examples of postural and support use variation due to the use of limbs providing balance support, a and b show the use of two sit postures used during feeding, c and d show two instances during bipedalism. These figures demonstrate the ability of balance to reduce the size of the supports required to bear the majority of the body weight of the animal. See Figure 5.1 and Table 5.1 for explanation of symbols.

5.2.2. Reliability of SMW data collection

Inter-observer reliability for this method was tested using five observers; one experienced in SMW for recording primate positional behaviour, two experienced in recording primate positional behaviour using standardized classification systems and two inexperienced in recording positional behaviour, but familiar with the concepts. The observers employed SMW to record a selection of postural and gap crossing behaviours from videos obtained during a year-long study of wild Sumatran orangutans *(Pongo abelii)* (unpublished data). The four inexperienced users of SMW were instructed in the use of the method for one hour, and

practiced the method for a further hour using video footage. The test involved observers recording 29 independent postures from videos. To simulate real-time data collection, observers were not allowed to pause or replay videos.

To compare the SMW figures drawn by the observers, each postural diagram was converted into 10 position values from the reference sphere (Fig. 5.2) which corresponded to the positions of the free end of the eight limb segments (left and right elbow, hand, knee and foot), the head and the ischia. Position values for equivalent segment and body parts from all postures were compared between pairs of observers using Cohen's Kappa (Cohen, 1960) and averaged to give an overall value of agreement. Cohen's Kappa is a conservative measure of agreement and takes into account the amount of agreement expected from chance alone, therefore the value obtained does not simply represent the percentage value measured accurately (e.g. agreement of 0.7 does not mean there was disagreement for 30 % of the observations). Overall, values of kappa range from 0 (no agreement between observers) to 1 (perfect agreement between observers), with values between 0.61-0.80 indicating substantial agreement.

Intra-observer reliability was tested using the same method on the most experienced user of SMW (JPM) who recorded the same 29 postures from video on two occasions, one month apart, to prevent postures being recalled from memory. Finally, the ability of observers to employ SMW to accurately record orangutan postures was validated, where possible, by directly measuring the limb and body-part angles from video frames and converting the angles

into position values using the sphere of reference. These were then compared to the position values obtained from the five observers.

5.3. Results

5.3.1 Reliability of SMW

The average Cohen's kappa value for inter-observer reliability was 0.700 (range 0.623-0.754). Cohen's kappa for intra-observer reliability was 0.785 and the average kappa value when comparing the video data to that of the observers was 0.638 (range 0.615-0.652). These results indicate substantial agreement according to Landis and Koch's (1977) scale after very little training, demonstrating the usability of Sutton Movement Writing for studies of primate positional behaviour.

5.4 Discussion

In this study we have assessed the ability of Sutton Movement Writing to permit more detailed recording of orangutan positional behaviour than previously possible. We found that SMW can be used with a high level of inter- and intra-observer reliability and provides results consistent with those obtained directly from video data. The high level of inter-observer reliability was achieved after a very short period of training, and is likely to improve with the level of training normally undertaken in field studies of positional behaviour (see Thorpe and Crompton, 2005). In comparison to other movement notation methods (e.g. Labanotation [see Hutchinson, 1996; Carlson, 2000] or Eshkol-Wachmann notation [Eshkol and Wachmann, 1958]), observers can be trained in the form of SMW used here relatively quickly, and it can

be recorded with greater ease and speed in the field. Sutton Movement Writing is likely to beneficial in a number of situations to answer more specific questions about positional behaviour and assist in its classification. Some of these are outlined below.

5.4.1 Recording previously unclassified behaviours: e.g. oscillatory gap crossing in orangutans

Traditional classification systems enable an overview of the majority of locomotor and postural behaviours performed by a species (e.g. Hunt et al., 1996; Thorpe and Crompton, 2006). However, in some instances behaviours have only been classified to a broad level using these systems. Furthermore, standardised systems require the observer to make a sometimes split-second decision regarding the classification and placement of a positional behaviour observed in the wild, within the pre-defined modes and sub-modes. Depending on the complexity of the behaviour and the experience of the observer, this may result in erroneous data. Therefore an alternative method is required by which the variation within previously unclassified behaviours can be captured under field conditions which are not always conducive to video recording.

Orangutans cross gaps in the forest canopy using a range of clambering and swaying gap crossing behaviours. Those that involve clambering across gaps using multiple limbs have been well described in the past (see e.g. Thorpe and Crompton, 2006) and are mostly used for smaller gaps where the animal can reach across to supports on the other side and transfer slowly across. In contrast, oscillatory behaviours, including sway, are mostly used to cross the larger gaps and are therefore considered key adaptations. In these, orangutans are able to use

support compliance to their advantage (Thorpe et al., 2007a), by either simply deflecting a branch with their body weight or by oscillating thin vertical tree trunks or branches backwards and forwards with increasing magnitude to cross gaps.

To date, however, oscillatory behaviours have only been recorded to the 'mode' level using traditional classification systems (see Thorpe and Crompton, 2006). This is partly due to the complexity of the behaviours involved as the animal makes subtle changes of its spatial position to emphasize the magnitude of the oscillation of the support. Oscillatory behaviours are also unusual because although they are a locomotor mode, it is actually the movement of the support, rather than the animal *per se*, that enables a gap to be crossed and the animal therefore tends to employ a range of postures to emphasize the movement of the support rather than different locomotor behaviours.SMW has the potential to be of considerable value in better understanding behaviours such as sway because they are essentially postural and also because, if the behaviour is sufficiently slow, sequences of positions can be recorded and the figures can be studied in detail at a later date to identify those that best described the behaviour. Furthermore, the details of the behaviour, including individual limb positions and use, together with additional contextual information such as multiple support use and the size of the gap crossed, can all be recorded with ease using SMW. However, through the use of SMW we were only able to record the main postures maintained during the movement of the support during each oscillation, not the postures or methods used to transfer onto or off the support (see chapter 6). If this level of detail from locomotor modes was required it may be best to obtain videos where possible, although SMW would then provide a suitable method to extract the information from the videos with a higher degree of resolution than traditional classification systems. Furthermore, SMW also provides a permanent visual record of what is

observed, and thus the data obtained can be used in various ways and the behaviours defined using different methods, or after discussion to obtain a wider consensus.

5.4.2. Classifying previously undefined behaviours and assessing postural variation

Once data regarding the variation within a previously unclassified behaviour have been obtained, some form of assessment needs to be undertaken in order to classify or group the behaviours. With previous classification systems, positional behaviours have been grouped based on a series of defining features and personal judgement (see Hunt et al., 1996; Thorpe and Crompton, 2006). These features include: the location of the main weight-bearing body parts; how the weight is borne (i.e. in suspension of compression) and the orientation of the torso. However, it is desirable to remove the element of subjective evaluation from this process as much as possible because, depending on the observer, differences in opinion can arise as to the placement of a particular posture or locomotor behaviour.

Data obtained using SMW may provide a more suitable input for quantitative methods to classify positional behaviours due to the ability to extract numerical data from the SMW figures. Once in a numerical form, the detailed limb position data from the SMW figures (i.e. the string of 10 numbers representing the positions of 10 limbs and body parts) can also be supplemented by information on the proportion of weight borne by the limbs, the method of weight bearing (suspension or compression), support use and contextual behaviour, also converted into numerical codes (see chapter 6 for an example). These data can then be explored using methods such as cluster analysis by which more similar postures or behaviours are clustered more closely together objectively based on a series of input traits such those

highlighted above e.g. limb position and weight (see Legendre and Legendre, 1998).This therefore provides a quantitative, objective approach for grouping postures for classification, rather than relying on the subjective views of the observer. Cluster analysis is not limited to the classification of postures, however, and could be used to see how variations within postures are related to support use or contextual behaviour through the addition of more traits into the original data matrices. This would facilitate more detailed comparison of, for example, changes in positional behaviour during ontogeny; laterality of different behaviours and differences in the positional behaviour of morphologically similar species living in different habitats or differences in the way in which morphologically distinct species exhibit the same behaviours (according to standardized classification systems).

5.4.3. Investigating the relationship between balance and weight-bearing limbs

Arboreal primates, particularly the large-bodied orangutan, have developed a range of complex positional behaviours in order to cope with the effects of support compliance e.g. using multiple supports and slow, un-patterned gait (see Thorpe and Crompton, 2005, 2006; Thorpe et al., 2009). In these instances the spatial arrangement of the limbs, both those bearing weight and those used for balance, is of particular interest, as balance achieved by touch is an important, yet understudied, component of positional behaviour. Balance control strategies are of particular interest in an unstable, arboreal environment in large-bodied species such as orangutans, as visual and vestibular systems are more likely to be disrupted. The movement of the habitat, both beneath their weight, and in the wind, and their ability to maintain postures at any orientation is likely to affect these systems, therefore increasing

instability. Therefore, balance is an important strategy, both to maintain stability and for safety in case of other supports breaking (chapter 7).

Traditional positional behaviour classification systems only record the use of the limbs bearing more than their own weight, therefore no information regarding the spatial arrangements of all the limbs, including those used for balance is obtained. Furthermore, as demonstrated by the SMW figures in Figure 5.3, the use of balance can have important implications for the supports used during particular behaviours. For example, Figures 5.3a and b, show the same posture, sit, but in Figure 5.3a a larger support is required to bear weight than in Figure 5.3b where the addition of limbs balancing on another support allow the animal to make use of a smaller weight-bearing support. Figures 5.3c and d demonstrate the same relationship, in this case during bipedalism, whereby the use of supports for balance enables progression on a smaller, more compliant support. Hand-assisted bipedalism is a key behaviour by which orangutans use multiple, compliant supports (Thorpe et al., 2007b), and yet the use of forelimbs for balance in addition to weight-bearing has rarely been studied in detail (see Thorpe et al., 2007b).

Sutton Movement Writing, therefore, provides an opportunity to study complex postures that involve multiple limbs for both weight-bearing and balance and that utilise multiple, flexible supports, where the fine tuning of limb positions is likely to impact on the behaviours possible. In such scenarios, slight adjustments of the position of a hand/foothold along a tapered branch enables orangutans to achieve subtle, but fundamental changes in spatial position and dampen or utilize support compliance according to requirements (Thorpe et al,

2009).Through the use of SMW we can begin to understand the role of these balance control strategies and how primates deal with support compliance to maintain stability in an arboreal habitat. This is of particular interest in larger bodied primates that may employ specific strategies in order to negotiate this niche successfully and safely.

5.4.4. Concluding remarks

From the examples provided above, Sutton Movement Writing appears to be a particularly useful means to clarify and classify the behaviours observed at the onset of a study, or when little is known about a species regarding the scope of their positional behaviour. Sutton Movement Writing can also be used to refine pre-defined classifications of complex behaviours that may consist of functionally different movements (e.g. tree sway; see chapter 6) and to increase our understanding of complex multi-limb, multiple-support behaviours. Furthermore, using SMW removes the need to decide the level of resolution at which the observers wishes to record positional behaviour at the beginning of a study, one of the biggest difficulties faced by an observer in primate field studies (Hunt et al., 1996). It therefore removes the risk of losing detail due to over conflation and enables the observer to re-visit the data later to extract more information if necessary.

Sutton Movement Writing, however, is not proposed as a replacement of the traditional classification systems, rather, we suggest, it should be used in conjunction with them. Both methods have their strengths and weaknesses depending on the needs of a particular study. For example, traditional systems will generally enable the collection of a larger data set, as the near-perfect visibility required by SMW is not as essential. However, SMW will enable the

finer details of more complex behaviours to be teased out, once they have been identified as playing a particular role in a species' positional behaviour repertoire. While SMW can be a useful method for recording postures and short sequences of slow locomotor behaviours, its application is limited when recording fast locomotion, due to the speed with which a series of postural figures can be drawn. In these situations, depending on the information required, either video (although this has its own limitations) or a traditional classification system would be more appropriate.

Overall, the aim of SMW to provide more detailed information of the relation between individual limbs and supports and the way they are used has been achieved. Furthermore, SMW data can be transformed into a numerical format, conducive to statistical analysis, which would allow quantitative analysis of complex positional behaviours, including the specifics of multiple limb use and the supports used. Such distinctions could be important in understanding subtle differences in kinematics, function and perhaps the cognitive challenges posed by the animal's habitat and would allow comparison both within and between species. Sutton Movement Writing may therefore facilitate greater understanding of how behaviours vary in response to the environment, and the specific means by which primates are able to perform key tasks in their particular habitat niches.

CHAPTER 6

DEFINING OSCILLATORY BEHAVIOURS IN ORANGUTANS: A NEW METHOD FOR THE CLASSIFICATION OF POSITIONAL BEHAVIOUR

Julia P. Myatt; Phillip Cassey; Robin H. Crompton and Susannah K.S. Thorpe

Oscillatory behaviours, as used by orangutans to cross gaps in their arboreal habitat, appear limited to use by the great apes due to their large body mass. Tree sway has been found to be an energetically beneficial mode of locomotion for orangutans, and yet the postures that possible facilitate the reduced energetic cost have yet to be recorded. We used a method of movement notation, Sutton Movement Writing, to record the spatial arrangement and use of limbs and support use during this unique and vital behaviour. Positional behaviours are usually grouped according to biomechanical rules based on the judgements of the observer, but the use of SMW provided an opportunity to cluster the data objectively based on key postural traits. Clustering analysis was employed to quantitatively group the behaviours observed based on their similarities. Limb position; the proportion of weight borne by a limb; the method of weight bearing and torso orientation were the input traits for analysis. Dendrograms were then created and relevant groupings established using homogeneity analysis. Overall, clustering analysis appears to provide a method by which positional behaviours can be grouped successfully, although it seems to be particularly appropriate for static postures. Furthermore, this method has the potential to assess the relationships between subtle changes in postural behaviours, habitat variables (e.g. support compliance) and context to further our understanding of how these large arboreal primates utilise their complex habitat.

JPM collected the data, analysed the data and wrote the manuscript; PC assisted with the data analysis. RHC contributed to original method development and SKST assisted with discussion of the statistical analysis and aided with the writing of the manuscript.

Key terms

Trait: refers to the variables selected to describe postures e.g. torso orientation.

Segment: refers to the separate body parts that make up the SMW stick-figure i.e. upper and lower arms, upper and lower legs, and the ischia, also referred to as the components of a figure.

Level: within each trait, each component can have one of a number of values, which are referred to as levels e.g. the proportion of weight borne by a limb can be one of three levels (nothing; weight; balance).

Distance: in the distance matrices, distance represents the difference between the levels within a trait e.g. a distance of two means the two levels are twice as different to each other as are two traits with a distance of one.

Dissimilarity: this refers to an overall measure of similarity or dissimilarity between two postures, based on the different distances between the different components of a trait. A dissimilarity matrix is a symmetric matrix that expresses the difference between all pairs of observations.

6.1 Introduction

The ability to cross gaps in the forest canopy safely and efficiently is a fundamental skill of all arboreal primates (Cant, 1992, 1994; Cannon and Leighton, 1994; Povinelli and Cant, 1995). Orangutans (*Pongo* spp.) use a number of gap crossing methods including bridging, transfer and sway (see Hunt et al., 1996; Thorpe and Crompton, 2006 for full definitions), with the latter involving the oscillation of compliant supports to move between tree crowns (Sugardjito, 1982; Sugardjito and van Hooff, 1986; Cant 1987a,b, 1994; Thorpe and Crompton, 2006; Thorpe et al., 2007a). These oscillatory behaviours appear limited to use by the great apes (see Sugardjito and van Hooff, 1986; Cant, 1994; Thorpe and Crompton, 2006; Thorpe et al., 2009), particularly orangutans, as both large body mass (adult male orangutans weigh 85 kg and adult females weigh 40 kg on average; Markham and Groves, 1990) and considerable mobility seem to be required (Thorpe et al., 2007a). These methods of gap crossing appear to be highly beneficial as tree sway has recently been shown to reduce the mechanical work needed to cross a gap, since it is an order of magnitude less costly than the orangutan descending to the ground and crossing terrestrially (Thorpe et al., 2007a). However, predation risk may act as a further pressure to adopt oscillatory behaviours, particularly on Sumatra where the presence of the Sumatran tiger (*Panthera tigris sumatrae*) may restrict use of the forest floor (Cant, 1992).

The two main oscillatory behaviours used by orangutans are defined as ‘sway’ and ‘ride’ (Thorpe and Crompton, 2006). Sway incorporates multiple active oscillations of the ‘vehicle’ support, which is the tree or liana oscillated, before gap crossing can be achieved whereas ride uses body mass to flex the vehicle support in one direction only (Thorpe and Crompton,

2006). Oscillatory behaviours are unusual in that it is mostly the movement of the support that enables the animal to travel, rather than the locomotion of the animal *per se*, and a range of different body postures are generally employed to actively assist support oscillation (Thorpe and Crompton, 2006). Nevertheless, despite the importance of these behaviours to the locomotor ecology of orangutans, the postures employed during oscillatory locomotion have yet to be defined or studied. By establishing definitions for this behaviour, below the mode level (see Hunt et al., 1996; Thorpe and Crompton, 2006), it would enable the relationship between the postural dynamics, supports used and characteristics of the gaps used during oscillatory behaviours to be studied in more depth. This would allow further investigation of the biomechanics and ecological importance of these unique and vital behaviours in orangutans. The first goal of this study, therefore, was to record the range of postures employed by orangutans during tree sway in greater detail than has been possible to date.

Most studies of primate positional behaviour have employed pre-determined classification systems (e.g. Hunt et al., 1996; Thorpe and Crompton, 2005, 2006; Bitty and McGraw, 2007; Wright, 2007; Prates and Bicca-Marques, 2008). These are initially based on key defining features including where and how body weight is borne and the orientation of the animal (Hunt et al., 1996). Biomechanically similar behaviours are then grouped based upon the judgments of the observer (Hunt et al., 1996; Thorpe and Crompton, 2006). However, because oscillatory behaviours achieve progression via postures and support movement rather than locomotion per se, they have proved difficult to describe using these systems. In contrast Sutton Movement Writing (SMW), originally designed for use in dance notation (Sutton, 1981), but adapted for use with primates by Myatt and colleagues (chapter 5), enables a visual representation of sequences of postures to be recorded instantaneously, and additional support

information to be noted. Furthermore, using SMW removes the need to decide on the level of resolution required to record positional behaviour at the beginning of a study, one of the biggest difficulties faced by an observer (Hunt et al., 1996). It therefore removes the risk of losing detail due to over conflation and enables the observer to re-visit the data later to extract more information if necessary.

To employ SMW to record the different postures exhibited during orangutan oscillatory gap crossing behaviour it is also necessary to develop techniques for interpretation and analysis of the figure drawings. To do this we explored the use of clustering analysis to quantitatively group the oscillatory postures recorded using SMW. Unsupervised clustering analysis is a method by which entities can be grouped based on either their similarity or dissimilarity in an objective manner, without prior knowledge of how they group (see Alexander, 1976; Kaufman and Rousseeuw, 1990; Everitt, 1993; Legendre and Legendre, 1998; Brock et al., 2008). This method is regularly employed in studies of evolutionary phylogeny (e.g. Brace at al., 2001; Coiffard et al., 2006), ecology (e.g. Legendre and Legendre, 1998; Petchey and Gaston, 2006) and genomics (e.g. Dudoit and Fridlyland, 2002; Brock et al., 2008). Specific traits of interest are selected and data from multiple traits combined to establish the level of similarity between postures based on distance metrics (e.g. Kaufman and Rousseeuw, 1990; Legendre and Legendre, 1998). Using such a method was particularly appropriate for this study as it enabled us to test how successfully postures can be grouped if the requirement for judgment regarding postural associations by the observer is removed; which is another possible problem with pre-determined classification systems. The overall aims of the present study were therefore to record oscillatory behaviour postures in orangutans in detail using

SMW and to assess how successfully new postures could be classified using an objective method, not previously applied to positional behaviours.

6.2 Method

The field study took place in the Ketambe Research Station (3° 41' North, 97° 39' East) located in the Gunung Leuser National Park (Leuser Ecosystem, Aceh Tenggara, Sumatra, Indonesia). The area consists of riverine terraces following the course of the Alas and Ketambe rivers and is covered mainly in primary, lowland rainforest (Rijksen, 1978; van Schaik and Mirmanto, 1985). The study took place between November 2007 and November 2008. The majority of data collection was carried out between February and November 2008, after a 5 week period of self-training had been undertaken by the observer (JPM). Self-training was carried out both to practice the use of SMW and to enable accurate estimation of heights, support diameters, support types and gap distances (by estimating and then measuring the variables). This process was repeated at frequent intervals during the field study to maintain accuracy.

The orangutans (*Pongo abelii*) at Ketambe have been studied since 1971 (Rijksen, 1978) and all individuals followed were fully habituated. Data were collected from both a focal orangutan (that was also the focus of another study) and others in the vicinity. Data were gathered both by whole day follows where the focal individual was followed from one night nest until it built its next night nest, and partial follows (where it was not possible to follow from nest to nest, but individuals could be followed for more than three hours). A focal

individual was followed for no more than four consecutive days, and on at least two separate occasions during the study period. Data were collected from 12 individuals (see Table 6.1).

Table 1. Study subjects

Age-sex class*	Name	Age (years)	No. focal days (full & partial)	Total no. of observations (sway & ride)
Flanged adult male	Dedi	Unknown	12	12
Unflanged adult male	SAM 1	Unknown	8	10
	SAM 2	Unknown	9	6
	Yop	30	4	2
Adult female	Yet	ca. 44	11	17
	Chris	21	13	14
	Sina	ca. 40	10	6
	Pluis	ca. 38	4	7
Sub-adult male	Yossa	16	4	3
Sub-adult female	Kelly	13	9	12
Juvenile female	Yeni	7	9	1
	Sari	7	1	1

*Age-sex classifications follow Wich et al (2004).

6.2.1 Data collection procedure

Data were collected using *ad libitum* sampling in which all occurrences of oscillation were recorded if and when possible. Gap crossing events may be broken down into 3 stages: 1) the orangutan transfers onto the vehicle support; 2) the orangutan moves across the gap, and 3) the orangutan transfers from the vehicle support to the destination support (the support used

immediately after the movement to continue progression). In the current study we focused on the postures maintained and supports used during stage 2, the movement of the vehicle support across the gap, as this is the main travelling portion of the movement and where support compliance is likely to present the greatest challenges.

Sutton Movement Writing (SMW; Sutton, 1981) was described in full in a previous chapter (chapter 5). It involves recording the postures observed using a stick-figure drawing (see Fig. 6.1 for an example). When the support was oscillated, the orangutans in this study tended to maintain one predominant posture - relative to the support - during the oscillation in each direction. Thus during ride only one posture was generally recorded, but during sway, where oscillations occur in both directions, multiple postures were recorded according to the number of oscillations employed. However, as the support bends across the gap, the orientation of the torso relative to the observer could change, as could the method employed to bear weight, for example, the posture may begin in an orthograde orientation with one of the hindlimbs bearing weight in compression, however, as the support bend over the torso becomes more pronograde in orientation and the hindlimb may change to bear weight in suspension as the animal hangs more beneath the support. Therefore, additional notes regarding these changes were made. If the posture did change substantially, however, in terms of limb position or in relation to the support, multiple stick-figures were drawn in sequence.

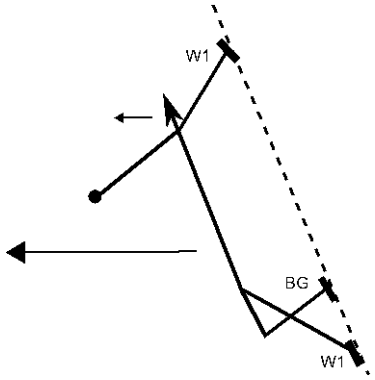


Fig. 6.1. Example of an oscillatory behaviour posture recorded using Sutton Movement Writing (SMW).The torso is represented by the arrow, with the arrow head indicating the position of the animal's head. The smaller arrow next to the head indicates the direction in which the animal is facing i.e. to the left in this example. The majority of body weight is borne by one forelimb in suspension and one hindlimb in compression as indicated by W1. The other hindlimb is assisting with balance (BG). The circle symbol at the end of the forelimb indicates that this limb is held in front of the coronal plane. The, thick lines at the ends of the other limbs indicates that they are behind the coronal plane. The support (dashed line) is shown next to the limbs utilising it.

For each SMW figure, a large arrow was used to indicate the main direction of travel in relation to the posture. Additional symbols were used to label the different limbs, including information about the proportion of weight borne by a limb (either nothing; utilised for balance i.e. not bearing more than its own weight; bearing more than its own weight but less than the majority of body weight; or bearing the majority of body weight). The mechanisms by which arboreal animals balance is an important component of arboreal life as they provide additional sensory feedback to assist in the maintenance of stability in an environment where visual and vestibular feedback may be disrupted (see Lackner et al., 2001; Coward et al., in prep). Therefore, information on the limbs that are used for balance is an important component of the SMW method. To provide a measure of limb segment position in three-

dimensions, symbols were used to represent whether a limb was in front or behind the coronal plane (see chapter 5). Additional information such as support details and gap size were also recorded, although this information was not used in the present study. Postures recorded using SMW were then converted into numerical data (see chapter 5 and details below) in order to carry out clustering analysis and thus sort the postures into groups based on their similarity.

6.2.2 Cluster analysis

Overall, the cluster analysis involved the following 6-step procedure, which is summarised here and described in detail below. 1) The traits (i.e. variables of interest) required to define the overall behaviour were selected. 2) Once chosen, distance matrices were created which provide a measure of the differences between the various levels within a trait. 3) Using the distance measures, overall dissimilarity matrices that quantify the differences between each observation (i.e. a posture) in a pair-wise manner for each trait were produced. 4) The dissimilarity matrices for all traits of interest were combined to generate an overall dissimilarity matrix. 5) From the overall dissimilarity matrix, a dendrogram was constructed, in this instance using agglomerative hierarchical clustering analysis, whereby groups were paired based on their similarity, combining successively larger groups until only one overall group remained. This dendrogram was used to visualise how the data are clustered. 6) In order to ascertain the number of functionally relevant groups to divide the tree into, homogeneity was plotted against the number of groups. Tree pruning was then performed to cluster the data into the relevant number of groups. Although this seems a rather long process, in practise it can be carried out with ease and relatively quickly. For more details of clustering analysis see Legendre and Legendre (1998).

6.2.2a Trait selection and creation of distance matrices

The traits used to define the postures observed were selected based on the key principles that are used to describe positional behaviour (see Prost, 1965; Hunt et al., 1996). These were: the proportion of mass borne by a limb/body part (although balance was also incorporated); whether a weight-bearing body part was in suspension or compression and torso orientation (following Hunt et al., 1996). In addition, the specific position of limb segments was included to describe the actual posture. The positions of all limbs were included, regardless of their function (limbs not contributing to support, those used for balance and those bearing body mass). The positions of limbs providing no functional support were included as these limbs may be important in shifting the mass of the animal, or reaching out for the destination support, thus providing more momentum during oscillatory behaviours. For each SMW figure there were nine components that effectively defined the properties of the different joint segments (i.e. position and function). These were the positions of the upper and lower arms, the upper and lower leg and the ischia. Each trait had a number of possible levels for each of the nine segment components for each SMW figure. As a consequence distance matrices were employed to code the distances between each level within a trait (Alexander, 1976). The most commonly used measure to compute distances between levels is the Euclidean distance which corresponds to the true geometrical distance between the points (Kaufman and Rousseeuw, 1990). However, as this study was based on categorical variables it was necessary to define the distances, or differences, between the levels separately as to which were more distinct than others. The levels for each trait and distance codes were as follows:

Proportion of mass borne by a limb: The proportion of body mass borne by each body segment was recorded as one of three levels: not bearing mass or touching a support; touching a support for balance but not bearing more than its own mass; or bearing more than its own mass. The difference between not touching a support and a limb bearing weight was allocated twice the distance as those between not touching a support and balance; and balance and bearing weight, based on the assumption that there is a functional difference between bearing weight (i.e. in terms of stress on the limb and muscle work), balance (not bearing more than its own weight), and doing nothing. This resulted in the distance matrix provided in Table 6.2.

Table 6.2. Distance matrix for the proportion of mass borne by a limb

Proportion of mass borne by limb		**0**	**1**	**2**
Limb not touching the support:	**0**	0		
Limb used for balance:	**1**	1	0	
Limb bearing more than own weight:	**2**	2	1	0

Method used to bear weight: The method of bearing mass i.e. whether a limb was in compression or suspension was also recorded for all segment components (i.e. all limbs plus the ischia) for weight bearing limbs. We opted to not account further for whether limbs used for balance were in suspension or compression as this would add another level of complexity to the study, and the method of balance is functionally less relevant than that used to bear weight. Thus, limbs not bearing weight or being used for balance were both coded zero. As the differences between the different possibilities were considered equal, they were all coded as one in the distance matrix.

Torso orientation: Torso orientation was recorded as one of five levels, defined by the location of the head relative to the torso (see Table 6.3 for definitions). This dataset therefore contained only one item of information. As there was a larger functional difference between

upright and downward torso positions compared to e.g. upright and sub-upright, differences between torso positions were allocated different codes in the distance matrix (see Table 6.3). Thus, the distance between upright and downward was allocated a score of 4, but the distance between upright and sub-upright was allocated a score of 1.

Table 6.3. Distance matrix for torso orientation

Torso orientation		**1**	**2**	**3**	**4**	**5**
Upright ($0^o \pm 22.5^o$)	**1**	0				
Sub-upright (22.5^o-67.5^o)	**2**	1	0			
Horizontal (67.5^o-135^o)	**3**	2	1	0		
Sub-horizontal (112.5^o-157.5^o)	**4**	3	2	1	0	
Downward ($180^o \pm 22.5^o$)	**5**	4	3	2	1	0

Limb position: Limb position was obtained from the SMW posture using a sphere of reference as described in chapter 5. In this system each segment was considered to consist of one fixed end (the proximal joint's centre of rotation e.g. the shoulder for the upper arm or elbow for the lower arm), and one free end (e.g. the elbow/wrist respectively). If the fixed end was taken as the centre of a reference sphere, then the relative orientation of the free end could be classified according to its position within the sphere in one of 26 pre-defined positions, situated 45^o apart (Eshkol and Wachmann, 1958). The position of the ischia was recorded relative the approximate centre of mass of the animal. As we did not want to differentiate between left and right limbs, all segments were coded using the right half of the sphere only (see chapter 5). In terms of distance allocation, as static postures, not movements between positions, were the input, each limb position was considered functionally the same as any other. Therefore, all distances were considered equal and scored as one in the distance matrix.

6.2.2b Creating the dendrogram

Using information provided in the distance matrices, dissimilarity matrices for all traits (proportion of weight borne by a limb, whether a weight bearing limb was in suspension or compression, torso orientation and limb position), for all postures were created in SAS (SAS Institute Inc. USA). A dissimilarity matrix describes the overall difference or similarity between each pair of SMW postures, for each of the nine components combined, based on the differences given in the distance matrix. A value of zero indicates absolute similarity. An overall compound dissimilarity matrix combining the four individual trait matrices was then created, with each of the four traits weighted as equally important. An equal weighting was most appropriate as there was no quantitative justification for weighting any of the variables as more important than any other when defining postural behaviour at this stage. Data were exported to R v. 2.10.1 (www.R-project.org) and a dendrogram (tree) of the combined dissimilarity matrix created using agglomerative hierarchical clustering with average linkage (see Kaufman and Rousseeuw, 1990; Legendre and Legendre, 1998). Agglomerative hierarchical clustering is a 'bottom-up' method that builds groups by fusing pairs of more identical postures at each step. Initially a group is a single posture, with groups increasing in size as more similar groups are paired together (see Kaufmann and Rousseeuw, 1990; Everitt, 1993; Legendre and Legendre, 1998). Average linkage defines the similarity between two groups and calculates the average of the similarities and differences between them (see Everitt. 1993; Legendre and Legendre, 1998). The overall dendrogram was visualised using FigTree v.1.3.1 (UK).

The next stage of analysis was to identify the most appropriate level of the hierarchy to classify the oscillatory postures, as dendrograms themselves do not indicate the 'ideal' number of clusters to define the behaviour. Visual analysis of the dendrogram is the most commonly employed method by which to detect clusters of interest or the optimum level for classification (e.g. Alexander, 1976). However, we explored the use of a quantitative method by which the most meaningful number of divisions could be identified based on multivariate homogeneity analysis (Bedward et al., 1992), rather than personal judgement. By plotting homogeneity against the number of groups (from one overall group, to all postures as individual groups) we were able to determine the point at which defining at a finer scale provided no further benefit (Bedward et al., 1992). This corresponds with the point at which an initial steep rise in homogeneity begins to plateau off, since the gradual rise in the plateau region after this indicates only minor variations within the major divisions (Bedward et al., 1992). Multiple 'steps' in homogeneity may occur before this final plateau, which indicates possible multiple levels of grouping. Once the numbers of relevant groups had been identified at the different points, the dendrogram was re-calculated, inputting the pre-determined number of clusters wanted in R v. 2.10.1 (www.R-project.org). This provided the most appropriate groupings of the data at relevant points to assist in identification of the suite of postural behaviours utilised during oscillatory behaviours in orangutans.

6.3 Results

In total, 89 postures utilised during oscillatory behaviours were recorded and used as input for the cluster analysis. The dendrogram of all four traits combined was created (Appendix IV) and the plot of homogeneity against the number of groups can be seen in Figure 6.2. Four sharp increases in homogeneity were identified, followed by a more gradual increase (note that the steep increase highlighting 3 groups as an important division was not included in this analysis as it refers to the initial branch divisions, which are too broad to be of interest for the classification of positional behaviour). The steep increase towards the end of the plot (labelled a) simply reflects the breakdown of groups into single observations, which were all different to some degree (e.g. the position of one limb segment) due to the small sample size, and was therefore also not relevant to our study. Thus, the substantial increases in homogeneity of note cluster the data into 6, 14, 18 and 22 groups; which will henceforth be referred to as tree 6, tree 14, tree 18 and tree 22 respectively. In each tree the main groups highlighted from the previous tree were partitioned further into successively smaller groups at each stage, although not all groups divided further at every level (Appendix IV).

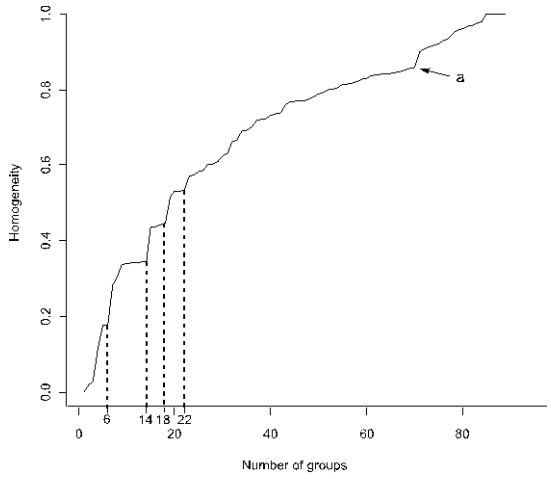
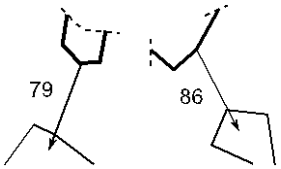


Fig. 6.2. Plot of homogeneity (based on the ratio of average within-group association between groups to the average association for the whole data set) against the number of possible groups. Steep increases in homogeneity point to optimum groupings and are highlighted. Point 'a' refers to the increase in homogeneity due to the small sample size that results in the majority of individual postures being different from one another.

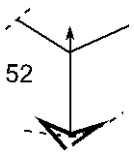
In order to visualise the different postures grouped at the successive levels and the reasons for their differences, basic stick figures (not including information about the method of weight bearing) of the individual postures were drawn. These are displayed in Figures 6.3-6.5 along with explanations of the common features of a group and an overall group name. Figure 6.3a-e shows the stick figures for the groups 1,2,3,5 and 6 from tree 6, and the further groupings within each cluster (from trees 14, 18 and 22). As group 4 was so large, the initial group from tree 6 is presented in Figure 6.4, together with the separate groups established in tree 14. The details of further divisions in trees 18 and 22 for group 4 are provided in Figure 6.5a-c. For example, initially group 4 was a general cluster of postures in tree 6 containing both compressive and suspensory postures with no clear defining feature. However, in tree 14 group 4b was identified as *hand-assisted orthograde compression,* based on its orientation and the bearing of body weight by the hindlimbs, in addition to assistance from the forelimbs.

This was further divided into the postures *monopedal compression (forelimb and hindlimb assisted)* and *bipedal compression* in tree 18 based on the difference in the number of hindlimbs used to bear weight. In tree 22, the group *bipedal compression* was further divided into *bipedal compression/forelimb suspend* and *bipedal compression (forelimb assisted),* based on their differences in the use of the forelimbs to either additionally bear a proportion of body weight, or to only assist with balance respectively.

a.

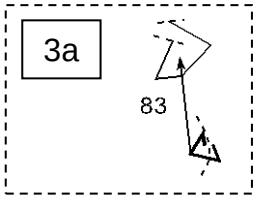
Group 1: *hindlimb suspend*- body weight borne exclusively by both hindlimbs in suspension	
1 	There was no further division of this group in trees 14, 18 or 22.

b.

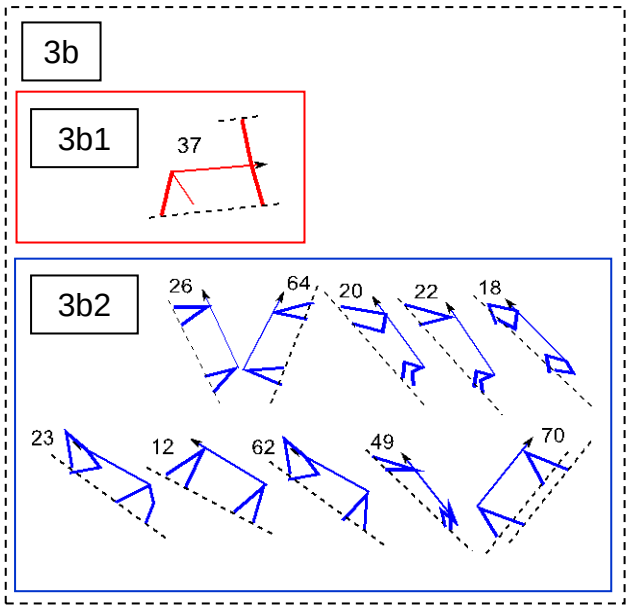
Group 2: *sit (forelimb assist)*- body weight is borne exclusively by the ischia, although the forelimbs may assist with balance	
2 	There was no further division of this group in trees 14, 18 or 22.

c.

Group 3: quadrumanous postures- all four limbs used to either bear weight or for balance in both compression and suspension



Tree 14, group 3a: *orthograde cling (forelimb suspend)*- body weight is borne only by the hindlimbs in compression, the forelimbs are used for balance. In group 3b, both forelimbs and hindlimbs are used to bear weight in compression and suspension.



Tree 14, group 3b: *pronograde quadrumanous postures*- all body weight is borne by all four limbs in both compression and suspension. Torso is pronograde in relation to the support.

Tree 18, group 3b1: *ipsilateral compression/forelimb suspend*- body weight is borne by one forelimb and one hindlimb on the same side of the body in compression and one forelimb in suspension. Torso is pronograde.

Tree 18, group 3b2: *quadrupedal compression*- all body weight is borne by all four limbs in compression. Torso is pronograde.

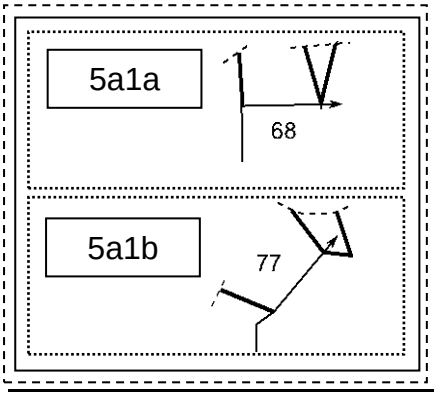
There was no further division of the groups in tree 22

d.

Group 5: forelimb/hindlimb suspension- all weight borne by two forelimbs and one hindlimb in suspension, no limbs used for balance

There was no division of this group in tree 14

There was no division of this group in tree 18

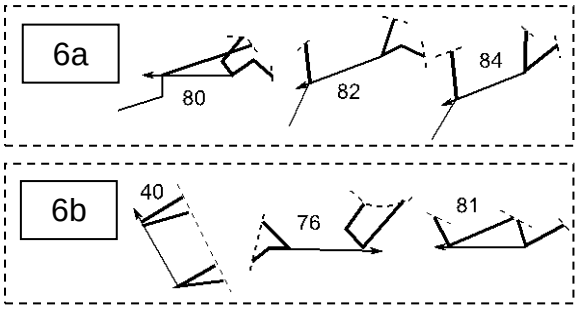


Tree 22, group 5a1a: *forelimb-hindlimb pronograde suspend*- Pronograde posture, facing downwards. Body weight is borne by both forelimbs and one hindlimb in suspension.

Tree 22, group 5a1b: *trunk vertical suspend*- Orthograde posture, facing sideways. Body weight is borne by both forelimbs and one hindlimb in suspension.

e.

Group 6: quadrumanous suspend- all weight borne by at least two hindlimbs and one forelimb in suspension, no limbs used for balance



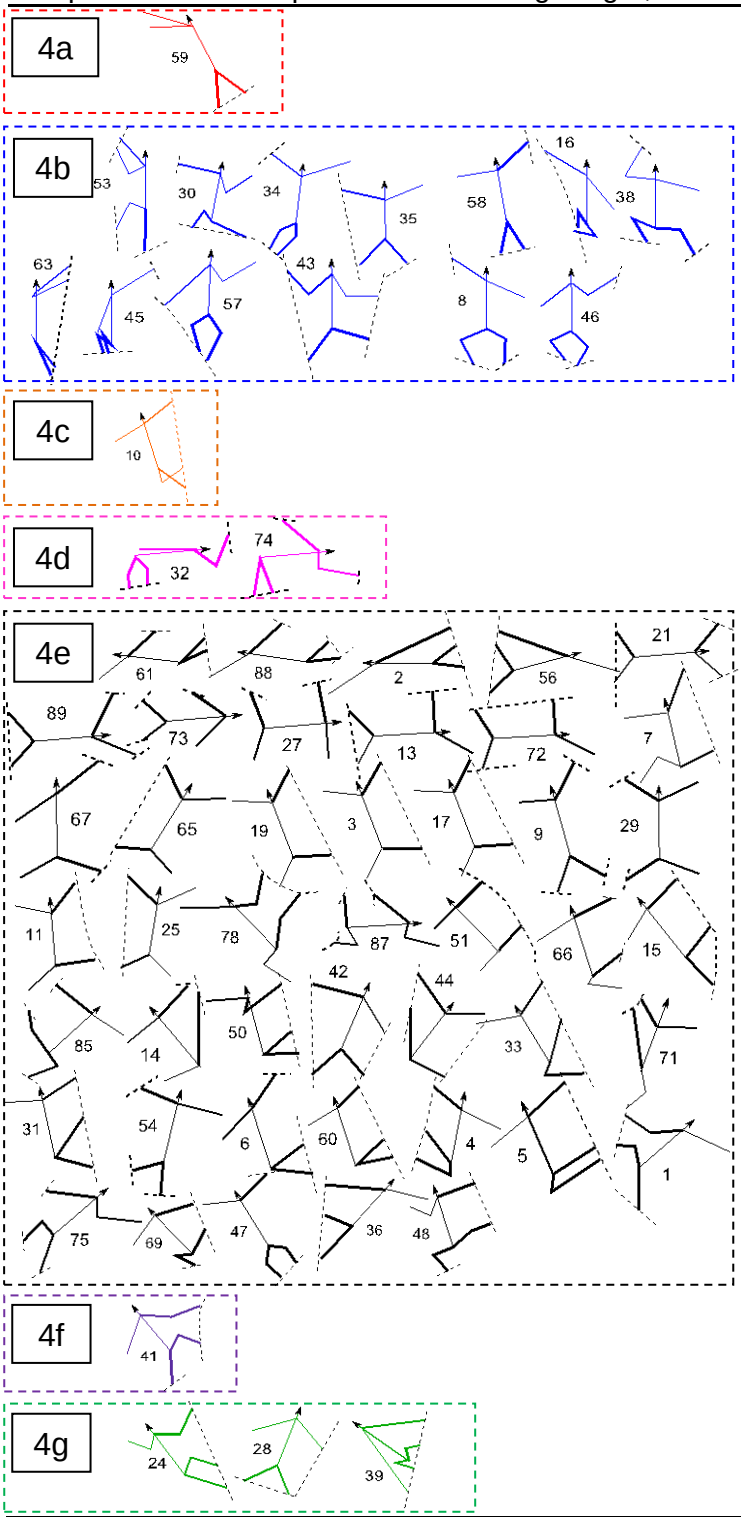
Tree 14, group 6a: *reaching quadrumanous suspend*- all body weight is borne by both hindlimbs and one forelimb in suspension.

Tree 14, group 6b: *quadrumanous suspend*- all body weight is borne by all four limbs in suspension.

There was no further division of this group at divisions 18 or 22.

Fig. 6.3. A simplified visual representation of the posture groups as allocated by the clustering analysis. Figures a-e represent groups 1-3, 5 and 6, as highlighted from tree 6 (Appendix IV). Within each figure the breakdown of the groups in the successive trees (tree 14, tree 18 and tree 22) are shown and discussed. Groups surrounded by dashed boxes are those formed in tree 14, those surrounded by solid lines and highlighted in different colours are formed in tree 18, and tree 22 divisions are represented by dotted boxes. The overall name given to the group is given in italics. If the group name is not in italics this represents a group that is too broad to be defined using one name. Within the posture figures themselves limbs bearing more than their own weight are highlighted in bold, details regarding the method of weight-bearing as ascertained from the detailed SMW figures are not included.

Group 4: suspensory/compressive postures- contains all postures using 3 limbs or less in both suspension and compression for bearing weight, limbs may also be used for balance.



Tree 14, group 4a: *bipedal compression*- all body weight is borne by both hindlimbs in compression, forelimbs are not used for weight-bearing or balance. Torso is orthograde.

Tree 14, group 4b: *hand-assisted orthograde compression*- torso is orthograde with the majority of body weight borne by the hindlimbs. Forelimbs may assist with weight bearing or balance.

Tree14, group 4c: *orthograde forelimb suspend/hindlimb compression*- body weight is borne in suspension and compression by at least one forelimb and hindlimb. Torso is orthograde.

Tree 14, group 4d: *pronograde stand/forelimb suspend*- body weight is borne by both hindlimbs in compression and one forelimb in suspension.

Tree 14, group 4e: orthograde and pronograde suspension- majority of body weight is borne by at least one forelimb in suspension and one hindlimb in suspension or compression. The remaining hindlimb may also bear weight in suspension or compression. Torso may be pronograde or orthograde.

Tree 14, group 4f: *orthograde ipsilateral suspend/hindlimb compression*- all body weight is borne by one forelimb and hindlimb in suspension and a hindlimb in compression.

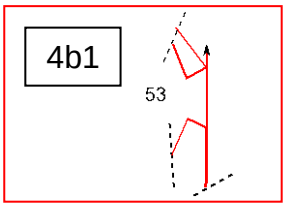
Tree 14, group 4g: *hindlimb compression/forelimb suspend*- body weight borne by both hindlimbs in compression and one forelimb additionally bears weight or assists with balance.

Fig. 6.4. A simplified visual representation of the group 4 (as highlighted in tree 6), showing the breakdown of the postures into different groups in tree 14, as shown by the coloured,

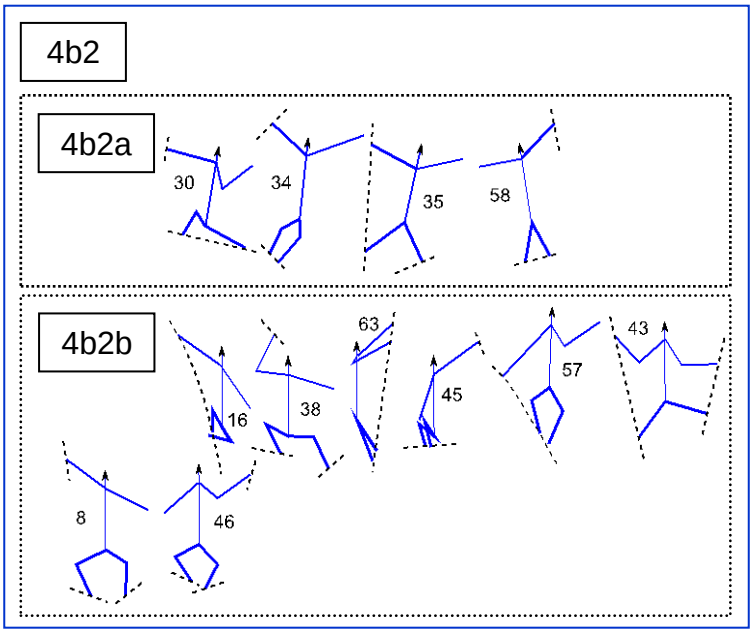
dashed boxes. The overall name given to the group is given in italics. If the group name is not in italics this represents a group that is too broad to be defined using one name. Within the posture figures themselves limbs bearing more than their own weight are highlighted in bold, details regarding the method of weight-bearing as ascertained from the detailed SMW figures are not included.

a.

Group 4b: *hand-assisted orthograde compression-* weight is borne by one or both hindlimbs in compression, forelimbs may bear weight or assist with balance. Torso is orthograde.



Tree 18, group 4b1: *monopedal compression (forelimb and hindlimb assisted)*- body weight is borne exclusively by one hindlimb in compression, both forelimbs and one hindlimb assist with balance. Torso is orthograde.



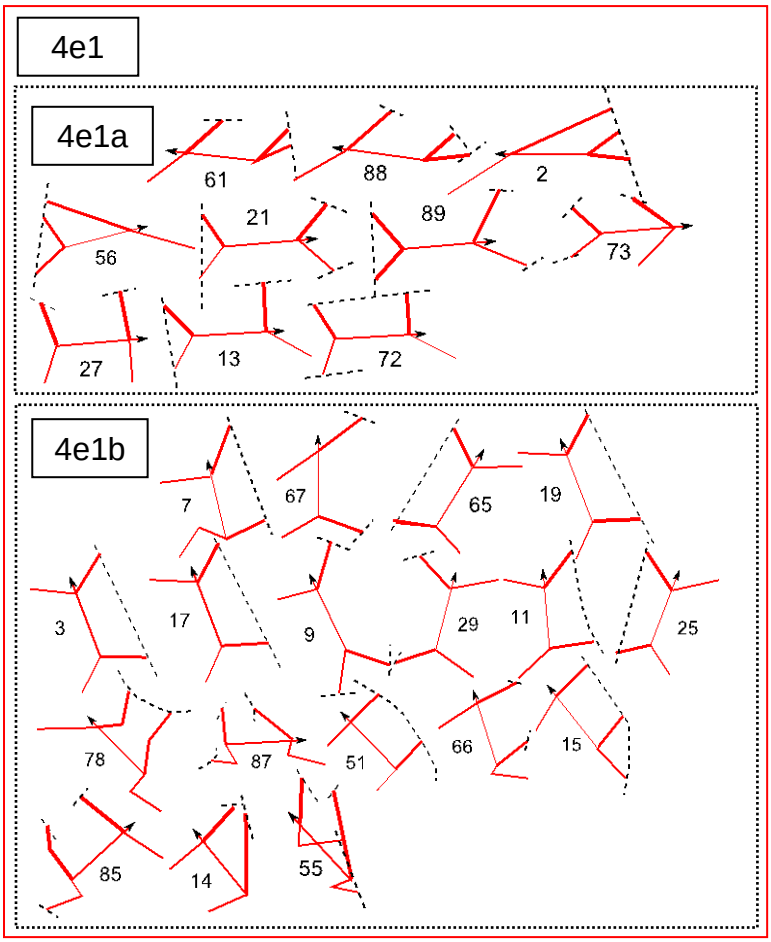
Tree 18, group 4b2: *bipedal compression*- body weight is borne predominantly by both hindlimbs in compression, forelimbs may bear weight or assist with balance. Torso is orthograde.

Tree 22, group 4b2a: *bipedal compression/forelimb suspend*- body weight is borne by both hindlimbs in compression and one forelimb in suspension.

Tree 22, group 4b2b: *bipedal compression (forelimb assisted)*- body weight is borne in compression by both hindlimbs. forelimbs assist with

b.

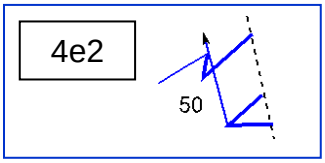
Group 4e: orthograde and pronograde suspension- weight is predominantly borne in suspension by at least one hindlimb and one forelimb. Torso may be pronograde or orthograde. Other limbs may assist with balance.



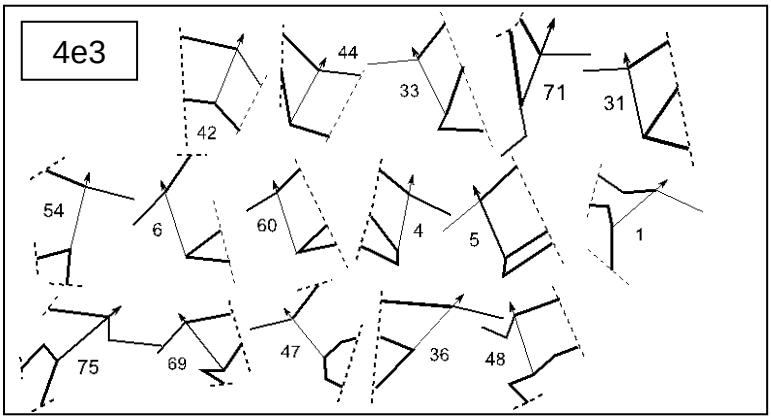
Tree 18, group 4e1: orthograde and pronograde suspension- majority of body weight is borne in suspension by at least one forelimb and one hindlimb, the remaining hindlimb either bears weight or assists with balance. Torso can be pronograde or orthograde.

Tree 22, group 4e1a: *forelimb-hindlimb suspend*- body weight borne in suspension by one forelimb and one hindlimb. The remaining hindlimb may also bear weight or assist with balance in either suspension or compression. Torso is

Tree 22, group 4e1b: *orthograde ipsilateral suspend*- all body weight is borne by one forelimb and one hindlimb in suspension. Remaining limbs may assist with balance. Torso is orthograde.



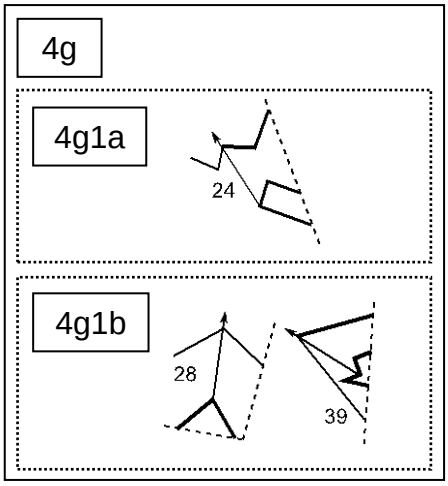
Tree 18, group 4e2: *orthograde suspend*: All body weight is borne by both hindlimbs and one forelimb in suspension. Torso is orthograde.



Tree 18, group 4e3: *orthograde ipsilateral suspend/hindlimb assist*: body weight is borne by the ipsilateral fore and hindlimb in suspension. The remaining hindlimb also bears weight in either suspension or compression. Torso is orthograde.

c.

Group 4g: *hindlimb compression/forelimb suspension*- weight is borne by at least one hindlimb in compression and a forelimb either bears weight in suspension or assists with balance.



There was no division of this group in tree 18

Tree 22, group 4g1a: *orthograde ipsilateral suspend/hindlimb compression*- body weight is shared between one forelimb and one hindlimb in suspension, the remaining hindlimb also bears weight in compression. Torso is orthograde.

Tree 22, group 4g1b: *hindlimb compression/forelimb suspend*: Majority of body weight is borne by both hindlimbs either in compression or cling. One forelimb may bear weight in suspension or assist with balance.

Fig. 6.5. A simplified visual representation of: a. group 4b; b. group 4e;c. group 4g (established in tree 14) and the further separation of the postures in these groups in trees 18 (shown by coloured, solid boxes) and 22 (shown by dotted boxes). The overall name given to the group is given in italics. If the group name is not in italics this represents a group that is too broad to be defined using one name. Within the posture figures themselves limbs bearing more than their own weight are highlighted in bold, details regarding the method of weight-bearing as ascertained from the detailed SMW figures are not included.

The division of a group at each successive level was due to a combination of differences in the traits, therefore, there was no single pattern of division across the different sub-groups and there was no clear division between modes and sub-modes as defined in traditional classification systems. In some instances the clustering resulted in only one division (e.g. groups 1 and 2), whereas in others there were several hierarchically-nested partitions at each

successive level e.g. group 4. Postures were initially divided in tree 6 partially based on the number of limbs bearing weight and what these limbs/body parts were e.g. sit, hindlimb suspend and quadrumanous (4 limbs) suspend. However, some groups at this stage e.g. group 4, contained a mixture of postures with no key defining feature, although more meaningful groups were established at successive levels in the hierarchy. This was particularly evident in the larger groups e.g. group 4, as this contained the most frequently used postures (*orthograde ipsilateral suspend*: 19.1%; *orthograde ipsilateral suspend/hindlimb assist*: 18.0% and *orthograde compression*: 14.6%) which used a combination of both orthograde suspension and compression. Overall, the majority of postures used during oscillatory behaviours were predominantly suspensory (64%), with the remaining bearing the majority of their weight under compression. Pronograde suspensory postures were also used relatively often (total 19%), although the different postures constituting pronograde suspension (*forelimb-hindlimb suspend*, *forelimb-hindlimb quadrumanous suspend*, *reaching quadrumanous suspend* and *quadrumanous suspend*) were not grouped together due to large differences in limb position and the number of limbs used to bear weight.

Further inconsistencies in the placement of specific postures within these groups, in addition to the placement of some overall groups, when viewed subjectively were apparent. For example, groups 4e1a and 4e1b both contain postures involving suspension from at least one forelimb and one hindlimb, but with the torso in a pronograde and orthograde orientation respectively. However, posture 87 which has a pronograde orientation was grouped within 4e1b, the orthograde group. Regarding overall group placement, group 4g contains two sub-groups that, based on personal judgement, would be more appropriately placed adjacent to other groups. For example, group 4g1a is defined as *orthograde ipsilateral suspend/hindlimb*

compression and yet is grouped separately from *orthograde ipsilateral suspend* (group 4e1b) at a completely different hierarchical level.

6.4 Discussion

The first aim of the present study was to record the oscillatory behaviours in orangutans using SMW, both to obtain the detail necessary to classify them quantitatively and to understand the use of oscillatory gap crossing behaviours in more detail. Sutton Movement Writing enabled the recording of detailed limb positions, together with the function of each limb i.e. the proportion of weight borne (including the use of balance), the method used to bear weight (i.e. compression or suspension) and details of the support used and gap crossing context. The extraction of numerical data from SMW is relatively straightforward and detailed and thus provides a means to quantitatively analyse the data. Therefore, in addition to being able to extract data for classification, data obtained using SMW would also enable the relationship between posture, support use, gap crossing context and age-sex class to be investigated, in addition to how subtle changes in the spatial arrangement of the limbs may influence the position of their centre of mass and thus the movement of the support (Thorpe and Crompton, 2006), although this would benefit from a larger sample size and thus we have not explored these relationships here.

Interestingly, we found some clear differences in the way in which the postures would have been clustered using traditional classification systems, compared to the clusters produced herein. For example, postures that would be defined as ‘squat’ using traditional systems (postures 45 and 16) were combined with those defined as ‘orthograde stand’ (group 4b; see

Hunt et al., 1996 and Thorpe and Crompton, 2006 for definitions). Both of these postures are orthograde with the majority of body weight borne by the hindlimbs, although the forelimbs may assist with balance. They differ in that the hindlimbs are tightly flexed next to the body in squat, whereas in bipedal stand the level of flexion can vary from flexed to completely extended. Therefore, when quantitatively comparing these two postures the only difference was the degree of limb flexion, rather than an overall combination of features. Furthermore, postures that would be defined as cling using traditional classification systems were also separated using cluster analysis, for example, in both posture 83 (group 3a) and posture 39 (group 4g1b) weight was borne by both hindlimbs in a cling position (tightly flexed, but using a vertical support; Hunt et al., 1996; Thorpe and Crompton, 2006). However, these two postures differed greatly in all other respects e.g. torso orientation, limb position and the use of other limbs for bearing weight and balance, thus raising questions about the key features used to define posture and the postures we traditionally group together. Using cluster analysis may, therefore, provide an alternative viewpoint from which to approach the classification of positional behaviour depending on the needs of the study.

Further differences were apparent due to the inclusion of information regarding the use of limbs for balance, and the positions of non-functional limbs in the present study. For example, postures fundamentally described as orthograde hindlimb compression were separated into three groups depending on the function of additional limbs; group 4a was bipedal compression with no assistance from other limbs, group 4b2a includes bipedal compression where a forelimb also bears weight, and this differs to group 4b2b where forelimbs are additionally used for balance, but not for bearing weight. If these differences were taken into account when investigating the relationship between posture, support use and gap crossing

context, the role of balance during these behaviours and its relation to habitat use could be understood in more detail.

The inclusion of the position of non-functional limbs did, however, result in some problems, as it caused postures to be clustered more closely together based on non-functional similarity than they would be using traditional systems, based on weight-bearing limbs only. However, it also highlighted some important differences. For example, group 6a and 6b are both forms of quadrumanous suspension, but group 6a differs from 6b in that one forelimb is free and reaching for the destination support. Such limb positions are likely to be important during oscillatory behaviours as they may provide momentum to the movement and also enable the orangutan to grasp the destination support earlier. This is key when crossing gaps in the canopy as it enables the distance that needs to be crossed to be shortened and possibly reduces the number of multiple oscillations required, thus reducing the amount of energy that needs to be expended (Thorpe et al., 2007a). Therefore, the inclusion of all limb positions for clustering analysis, in this instance, has hinted at some interesting differences in postures and demonstrates the possible relevance of limb function other than bearing weight when describing particular positional behaviours.

Originally, the primary aim of this study was to remove the element of subjectivity when classifying positional behaviour. Overall, clustering analysis was successful at providing meaningful postural groups of oscillatory behaviours; although some inconsistencies in posture placement were apparent when observer judgment was taken into account e.g. posture 87. This was likely due to the method of clustering employed (agglomerative hierarchical

clustering), as this joins two postures together based on their combined similarity from the range of traits, but once grouped two postures cannot be separated, even if a re-assessment of the grouping would be beneficial after the initial stage. Therefore, if they are more similar in a non-functional trait e.g. limb position, but differed to a greater degree (based on the distances provided in the matrix) in a functional trait, they would still be grouped together. In the case of posture 87, it appears to be very similar to posture 78 in relation to limb position and thus this high level of similarity would have joined them at the first level, regardless of their different torso orientations, resulting in posture 87 ending in a less suitable group overall. To overcome this issue the separate traits could be weighted such that limb position did not have as large an impact on the groupings as the other traits, for example. This was not employed in this study as we had no apriori justification for attributing different weightings before undertaking the analysis. However, it may be more appropriate when defining behaviours in future studies to weight limb position as less important than the other traits as this is the trait that appeared to result in the most erroneous groupings.

A further problem with clustering analysis was identified, although this was more specific to its use with oscillatory behaviours. As only one moment in time (i.e a static posture) can be entered for clustering analysis any changes in torso orientation relative to the observer, or changes in the method of bearing weight (e.g. a hindlimb may change from bearing weight in compression at the start of the movement but end bearing weight in suspension as the support bends over) that may occur during the movement cannot be taken into account. In the present study, postures were recorded predominantly at the mid-point of the movement, in order to reduce some of the discrepancies that may occur due to this variation and this issue was also taken into account when assigning names to the groups of postures defined. For example,

torso orientation was defined in relation to the support and the limb positions, rather than the view of the observer, as this usually remained relatively unchanged during the movement. This is demonstrated with the postures in group 3b2 (Fig. 6.3c) that were defined as pronograde because the support was bent beneath their weight in a pronograde fashion (Myatt, pers. obs), despite the fact that their torso was orthograde relative to the observer.

Overall, however, the use of clustering analysis in the present study demonstrates the possible applicability of such a method when applied to positional behaviour and its ability to group positional behaviours in a less subjective manner. The actual postures employed during oscillatory gap crossing behaviours encompassed a wide range of postures, including compression and suspension and both orthograde and pronograde orientations. The majority of these postures overlapped with those observed during the general positional behaviour repertoire of orangutans (Thorpe and Crompton, 2006), although not all could be described adequately using the previously defined sub-modes, and new classifications were created. For example, *orthograde ipsilateral suspend* and *orthograde ipsilateral suspend/hindlimb assist* were clustered into two separate groups and employed in 37.0% of the observations overall. Using traditional classification systems these postures would have been subsumed under the sub-mode 'trunk vertical suspend' (Thorpe and Crompton, 2006) even though there is a fundamental difference in the role of one hindlimb which may have functional implications for the movement. This study, therefore, highlights the importance of assessing previously undefined behaviours external to the constrictions of a pre-determined system as behaviours rarely observed during the overall repertoire of a species, may play a key role in more specific behaviours.

The high frequency of orthograde ipsilateral postures during oscillatory behaviours may be because at least one forelimb and possibly one hind limb remain free throughout the motion and are therefore available to grasp supports in the destination tree. Suspensory postures are also considered beneficial to larger arboreal primates as they theoretically reduce the risk of falling because body mass is already positioned below the support (Grand, 1972; Cartmill, 1974, 1985; Cant, 1987 a, b; Hunt, 1992a). Such a capacity may be particularly important during oscillatory behaviors since, as they are a gap crossing behaviour, they involve the use of compliant supports in the outer canopy of rainforest trees, where there are likely to be few other supports which could be used to brake a fall.

In addition to the use of orthograde suspensory postures, pronograde suspension also formed the basis of three defined groups (*forelimb-hindlimb suspend*, *reaching quadrumanous suspend* and *quadrumanous suspend*) and was employed in 17.9% of the observations. Pronograde suspensory behaviours appear to be unique to orangutans (Thorpe and Crompton, 2006; Thorpe et al., 2009) and during locomotion and feeding they have been associated with compliant support use (Thorpe et al., 2009; chapter 7). Their use during sway behaviours may also be related to their ability to enable the use of smaller supports that are often present in the small trees used for oscillatory behaviours (Myatt, unpublished data). Further study of the use of these different postures and the gap crossing context in which they occur may also shed more light on these relationships, and any further benefits conferred by pronograde suspension during oscillatory behaviours e.g. the ability to cross larger gaps. The presence of pronograde suspension during key gap crossing behaviours may further support the suggestion that they arose after orangutans separated from the last common ape ancestor, possibly as a specialization to cross increasing numbers of gaps or to increase effectiveness in

traversing the canopy as orangutans became more restricted to a continuous-canopy arboreal lifestyle (Thorpe et al., 2009). Therefore, investigating its specific role during oscillatory behaviours is an important next step.

Overall, the SMW method was found to be suitable for recording sway postures in detail and enabled us to see how the postures clustered based on quantitative rather than qualitative measures. Clustering analysis appears to be an effective method that enables the more subtle differences in positional behaviour to be extracted and permitted the classification of sway postures for incorporation into future field studies. While clustering analysis may not be suitable for use with all behaviours due to its requirements for static data as the input, it does provide an opportunity to further investigate the variation that occurs within positional behaviours. For example, it may be appropriate for investigating the level of postural variation within a pre-determined locomotor mode, and could be used to assess the level of complexity within a single mode regarding the range of postures observed, as was employed here. Clustering analysis, however, also has benefits beyond simply grouping similar postures together for classification systems. If the approach employed here was expanded to include details of support use or contextual behaviour as additional traits, then dendrograms could be produced that would allow objective quantification of the full relationship between the animal and its locomotor environment. This could, for example allow detailed analysis of the use of oscillatory behaviours in orangutans in terms of the supports used, the gap crossed and the age-sex class of the individual to investigate the effects of body mass during these behaviours. It could also be used to assess the use of oscillatory behaviours in the other non-human apes, as although the use of tree sway in chimpanzees and gorillas has been referred to (Doran, 1993a, b; 1996; Remis, 1995), their use has yet to be studied. Furthermore, it could also be

used to better understand the relationship between compliant arboreal supports and how they are employed during different behaviours e.g. feeding, including the role and importance of limbs used for weight-bearing or balance. By employing clustering analysis, one could also assess whether particular posture and support size combinations grouped together, or were used for certain behaviours. Finally, we anticipate that it could be of value in understanding subtle differences in the locomotor ecology of closely related species (see chapter 5, for discussion).

In conclusion, therefore, the combination of SMW recording and cluster analysis provides an alternative method by which the classification of positional behaviours can be explored. Although, the method used here has revealed some potential problems, other avenues of clustering analysis and the methods used to produce the dendrograms could be explored to refine the method. The use of clustering analysis could also be extended to incorporate other aspects of positional behaviour, including habitat variables, to provide an overall understanding of subtle nuances of positional behaviour and how it is used in the complex arboreal environment.

CHAPTER 7

POSTURAL STRATEGIES EMPLOYED BY ORANGUTANS (*Pongo abelii*) DURING FEEDING IN THE TERMINAL BRANCH NICHE.

Julia P. Myatt and Susannah K.S. Thorpe.

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Obtaining food in an arboreal habitat is complex due to the irregular and flexible nature of the supports available. As the largest, predominantly arboreal primate, orangutans are expected to have developed particular postural strategies to enable them to feed successfully. In particular, they need to be able to cope within the terminal branch niche (TBN) as this is where the smallest, most compliant supports are, and also where the majority of the fruit and leaves are situated. We recorded feeding posture, along with a number of ecological and behavioural variables from different age-sex classes to enable analysis of the interactions between these and the compliance of the supports (as estimated from stiffness score). Suspensory postures with a pronograde orientation were used on the most compliant supports for all age-sex classes, and appear to play a particular role in facilitating safe use of the TBN by distributing body weight and using limbs for balance across multiple supports. Adult males appear to use the same postures and feeding zones as the other age-sex classes, but appear to use stiffer supports where possible due to their larger body mass. Feeding method and feeding bout stage differed between the age-sex classes in relation to support stiffness, with larger adult males taking fewer risks due to their larger size, compared to infants and juveniles. The feeding behaviour of adult females, however, appears to be influenced by social factors in relation to the behaviour of dependent offspring.

JPM developed the method, collected the data, analysed the data and wrote the manuscript. SKST assisted with the analysis of the data and the writing of the manuscript.

7.1 Introduction

Food acquisition is one of the major determinants of reproductive success for all animals (Cant, 1992). Numerous areas of research have stemmed from a desire to understand the influence of feeding on the behavioural ecology of the non-human apes, such as studies of feeding activity budgets (e.g. Masi et al., 2009; Morrogh-Bernard et al., 2009), ranging patterns, and the role of fallback foods (e.g. Marshall et al., 2009; Vogel et al., 2009). More specific studies have also focused on the mechanical properties of food in relation to jaw structure (e.g. Taylor et al., 2008; Vogel et al., 2008) and its nutritional content (e.g. Hohmann et al., 2010; Loyola et al., 2010). Studies of social interactions in relation to feeding behaviour (e.g. Utami et al., 1997; Robbins et al., 2009; Jaeggi et al., 2010), together with the use of tools, and the evolution of culture are also prevalent (e.g. van Schaik, 2003; Lonsdorf et al., 2009; Sanz et al., 2010) .

Arboreal primates, however, not only need to know where to find food and how to process it, but also need to negotiate a complex arboreal environment in order to access food patches. The canopy of tropical forest is characterised by irregularly spaced and angled supports, which also vary in their compliance (flexibility). The terminal branch niche (TBN), at the periphery of tree crowns, poses particular problems because this is where the majority of high quality fruit and leaves are situated (Grand, 1972; Houle et al., 2007), but it is also where the smallest and most compliant supports are found (Grand, 1972; Cant, 1992). For orangutans, moving and foraging within the terminal branch niche is expected to be particularly difficult as their large body mass increases the likelihood of arboreal supports bending and breaking.

Thus the ability to use relatively plastic postural behaviours that enable the exploitation of feeding patches throughout the canopy is likely to be key to their success.

Orthograde (trunk vertical) suspensory postures are thought to be one of the primary mechanisms by which large-bodied apes solve the problems of terminal branch feeding (Grand, 1972; Cartmill, 1985; Cant, 1992). Although smaller bodied monkeys such as *Macaca spp*. are able to feed in the TBN using above-branch, compressive postures (Grand, 1972; Dunbar and Badam, 2000), as support diameter decreases or as body mass increases it becomes more difficult to maintain balance on the top of the branch (Cartmill, 1985). Instead, by suspending beneath the support, apes enhance stability because they have in effect already fallen off (Cartmill, 1985). What little field data exists on this topic does suggest a strong relationship between feeding and suspensory postures for the non-human great apes; 96% of observed arm-hanging occurred during feeding for male and female chimpanzees (Hunt, 1992a) and bonobos also use similar behaviours (Doran, 1993a; Fleagle, 1999). Gorillas use suspensory locomotor behaviours to access food in the TBN (Remis, 1995), although they rarely use arm-hanging postures to feed (Fleagle, 1999) and gibbons use both seated and suspensory postures when feeding. Orangutans, as the most arboreal of the great apes, frequently use a range of suspensory postures during feeding (Cant, 1987a, b) and both adult males and females increased their use of suspensory behaviours on smaller supports when feeding on *Ficus spp* (Cant, 1987a).

If suspension is a primary mechanism for large-bodied apes feeding in the TBN, one would also expect to see an increased amount of suspension in species and individuals of larger body

mass (Cartmill and Milton, 1977; Cant, 1992). Data from interspecific field studies however are rather limited and inconclusive; larger-bodied siamangs used suspensory arm-hanging more than gibbons (Harvey et al., 1986), but gibbons were found to use suspension approximately three times as often as chimpanzees (Hunt, 1991). This might suggest that there is a body mass threshold above which animals are forced to use larger supports and therefore less suspension (see Grand, 1972, 1984; Ripley, 1979). Adult male orangutans were found to use compressive postures such as sit and stand more than adult females (Cant, 1987a) and females were observed to use suspensory postures more than males when feeding on figs in Thorpe and Crompton's (2009) study. Cant (1992), however, found that as body mass increased across the different age-sex classes, so did the size of the supports used, but there was no difference in the amount of suspension. Support use differences were also observed in gorillas, with adult female gorillas using smaller supports and the TBN more than adult males (Remis, 1995). These differences may be related to safety, as the risk of falling increases with increasing body mass (Cartmill and Milton, 1977; Cant, 1992). Overall, these results suggest that animals of different body mass may use supports of different sizes or feed in different parts (zones) of trees, but whether they use varying postures remains unclear.

Although a number of studies have touched on the relationship between great ape feeding postures and habitat use (e.g. Hunt, 1992a, b; Doran, 1993a, b; Remis, 1995; Thorpe and Crompton, 2009), few have addressed the subject comprehensively. Orangutans are of particular interest as they are the only large-bodied ape to forage exclusively in the forest canopy and we might therefore expect adaptations for TBN feeding to be particularly prevalent in this species. To date, of the three studies of orangutan feeding posture and habitat use (Cant, 1987a, b; Thorpe and Crompton, 2009), Cant's (1987a) study was based on only

three adult females and one adult male feeding on one food type (figs), over a short time period and while Thorpe and Crompton's (2009) study was more thorough, there was substantial variability between the two studies. Furthermore, none of the studies have integrated additional feeding variables into their study, although they have hinted at other factors that may influence orangutan behaviour. For example, feeding technique was highlighted by Cant (1992) as an additional complicating factor that could also impact on the postures observed or the supports used. Thorpe and Crompton (2009) also noted that flanged adult males often used different feeding strategies to the other age-sex classes e.g. breaking off food branches and moving to stable supports to eat them, rather than eating food at the source and Dunbar and Badam (2000) found that feeding method influenced the postures maintained by bonnet macaques (Dunbar and Badam, 2000).Therefore the physical ability to obtain the food items may play a key role in posture or support selection.

The aim of this study therefore was to further investigate the relationships between the compliance of the supports utilised, the postures used and other ecological and behavioural variables that may influence feeding behaviour in orangutans of different age-sex classes. Specifically we hypothesise: 1) that suspensory behaviours will play a specific role during feeding in orangutans; 2) that the use of suspension will increase as support compliance increases; 3) that pronograde suspension may enable feeding on the smallest supports in the TBN as it has been found to enable locomotion on these supports (Thorpe et al., 2009); 4) that there will be age-sex differences, either in the use of suspensory postures (as predicted by Cartmill and Milton, 1977; Cant, 1992), or in the use of supports (size, number and location within the canopy; as proposed by Grand, 1972, 1984; Ripley, 1979) and 5) that differences in feeding behaviour will influence the compliance of the supports used in combination with the

postures observed and age-sex classes using them due to the different physical abilities required to obtain different food types in different ways. Overall, this paper expands on a previous studies of orangutan locomotion and support stiffness (Thorpe et al., 2009), to ask how they deal posturally with support compliance during another crucial, and selectively important behaviour; feeding.

7.2 Method

7.2.1 Field Study

The field study took place in the Ketambe Research Station (3^{o} 41' North, 97^{o} 39' East) located in the Gunung Leuser National Park (Leuser Ecosystem, Aceh Tenggara, Sumatra, Indonesia). The area consists of riverine terraces following the course of the Alas and Ketambe rivers, covered mainly in primary, lowland rainforest (Rijksen, 1978; van Schaik and Mirmanto, 1985). The study took place between November 2007 and November 2008. The majority of data collection was carried out between February and November 2008, after a 5 week period of self-training had been undertaken by the observer (JPM). Self-training (estimating and then measuring the variables) was carried out to enable accurate estimation of support diameters and support types. This process was repeated at frequent intervals during the field study to maintain accuracy.

The orangutans (*Pongo abelii*) at Ketambe have been studied since 1971 (Rijksen, 1978) and all individuals followed were fully habituated. Data were collected from 14 individuals, consisting of both adult and immature orangutans (see Table 7.1 for subject information). A

single focal individual was followed for a maximum of four consecutive days on at least two well-separated occasions during the study period. This reduced any bias due to an abundance of a particular food type during one observation period, although orangutans at Ketambe have relatively stable diets that do not differ significantly between seasons (Wich et al., 2006). Individuals were followed from one night nest until the next night nest, although data were also collected from partial follows (where it was not possible to follow an individual from nest to nest, but were followed for more than three hours).

Table 7.1 Study subjects

Age-sex class	Name	Age (years)	No. focal days (full and partial)
Flanged adult male	Dedi	Unknown	12
Unflanged adult male	Sam 1	Unknown	8
	Sam 2	Unknown	9
	Yop	30	4
Adult female	Yet	ca. 44	11
	Chris	21	13
	Sina	ca. 40	10
Sub-adult male	Yossa	16	4
Sub-adult female	Kelly	13	9
Juvenile female	Yeni	7	9
	Sari	7	1
Infant male	Pele	4	4
Infant female	Cani	5	7

*Age-sex classifications follow Wich et al (2004).

Instantaneous sampling on the 1-min mark was used to record all observations of postural data. Data were collected using Sutton Movement Writing (SMW) adapted for use with orangutans, as described elsewhere (chapter 5). SMW is a form of dance notation (Sutton, 1981) and involves the recreation of a posture as a stick figure. The 3D positioning of limbs was notated using symbols, along with information about the direction the animal was facing and the proportion of weight borne by the individual limbs, or if they were used for balance. Limb loading was estimated from the amount of support deflection beneath the mass of a limb, along with its position and the amount of tension in the limb.

A posture was counted when an individual did not alter the position of its main weight-bearing body parts for longer than 5 seconds. For this study only postures exhibited when animals were obtaining and eating food were included in the analysis. As postures frequently last longer than the 1 minute sampling interval employed here, this can result in a series of non-independent postures. In these instances, one posture was selected at random from the sequence for inclusion. Additional data (see Table 7.2) recorded alongside the basic posture included support diameter class (following Cant, 1987a) and support type for each body part in contact with a support. Tree zone was also recorded, tree zones one to four follow Cant et al. (2001) and refer to the centre of the tree, working out towards the periphery of the tree crown respectively. Additional zones were included to describe other areas used by orangutans during feeding. These included: lianas growing between trees (zone 5) and the use of all zones at once (zone 6), where the animal could hold onto the trunk of a tree, whilst obtaining food from the terminal branch niche. A range of feeding behaviour variables were also incorporated, these included: food type (following standard categories used for orangutans after e.g. Russon et al., 2009), feeding method which refers to the physical method

used to obtain the food (e.g. removing it from the branch), feeding bout stage and food location (see Table 7.2 for further details).

Table 7.2. Observational data recorded

Data	Description
1. Date	
2. Name	
3. Time	Time, on the minute point
4. Posture	Recorded using Sutton Movement Writing (Myatt et al., in prep), defined as: *hindlimb suspend*- all body weight borne in suspension from both hindlimbs; *forelimb-hindlimb suspend*- suspension from one forelimb and one hindlimb, torso is pronograde and on its side; *orthograde forelimb suspend*- body weight borne in suspension from one or both forelimbs; *orthograde quadrumanous suspend*- body weight borne in suspension by a combination of fore and hindlimbs, torso is orthograde; *pronograde suspend*- body weight borne in suspension by any combination of fore and hindlimbs, usually 3 or more, torso facing towards or away from the support; *squat*- body weight borne in compression by hindlimbs in a tightly flexed posture; *orthograde stand*- body weight borne in compression by hindlimbs in extended or slightly flexed positions; *sit*- body weight is borne predominantly by the ischia; *cling*- similar to squat but using a vertical support; *pronograde stand*- body weight borne by 3 or more limbs in compression, torso is pronograde; see Hunt et al., 1996; Thorpe and Crompton, 2006 for full descriptions.
5. Support diameter	<2 cm; ≥2<4 cm; ≥4<10 cm; ≥10<20 cm; ≥20<40 cm; ≥40<60 cm (following Cant, 1987).
6. Support type	trunk; branch; liana; other (e.g. nest).
7. Tree zone	1: trunk and other supports; 2: major branches; 3: intermediate branches; 4: terminal branches; 5: lianas between trees; 6: across all zones (following Cant et al., 2001).
8. Food type	Fruit (including figs and seeds); leaves (including plant stems); insects; bark; other (e.g. flowers, meat)
9. Food location	above (above head); same (below head and above hip); below (below hip height).
10. Feeding method	ABR (removing individual food items from a branch); ABM (holding an attached branch directly to the mouth to remove items); BBM (breaking off a section of branch and holding it to the mouth to remove items); HBR (holding an attached branch in place using one limb and removing individual items with another limb); BKM (feeding on bark using the mouth as the main manipulator); BKL (feeding on bark using limbs as the main manipulator); ILe (feeding on insects from a bundle of leaves); IL (feeding on insects directly using the limbs); other
11. Bout	R: reach/search; B: bring back (bring an item back to feed on, not including travel); E: eat

7.2.2. Statistical analysis

To enable analysis of multiple ecological and behavioural variables in addition to posture, the SMW figures were converted into standardised pre-classified postures (Hunt et al., 1996; Thorpe and Crompton, 2006; see Table 7.2 for brief description).The additional details obtained using SMW will be used in a future study. Classification using standardised systems is based on torso orientation and whether the limbs bearing body weight are in suspension or compression. It was therefore simple to convert from the SMW figures into the standard categories. Due to the small sample size postures were classified to the mode level, rather than sub-mode (Hunt et al., 1996; Thorpe and Crompton, 2006) to facilitate statistical analysis. Individuals were also conflated into adult males (including both flanged and unflanged but sexually active adult males); adult females; sub-adults (male and female) and infants and juveniles (males and females of both classes) to increase sample sizes.

To provide a measure of the compliance of the supports, the continuous response variable, stiffness score (SS; Thorpe et al., 2009) was calculated for each observation. This is essentially a measure of the mean stiffness of all the supports used during a positional behaviour bout, based on support diameter and the number of supports used to bear weight (Thorpe et al., 2009). Stiffness score was calculated for postures in which one to four supports were used as it was not possible to record support information when more than four supports were used due to vision and the volume of information recorded for each. Stiffness score was calculated as:

Equation 7.1. $\ln(SS) = \ln(\sum Y_i/n)$

where Y_i is the interval mid-point for each diameter category (see Table 7.2), for the *i*th support used and *n* number of supports bearing weight. Natural log was used to transform SS and provide a continuous variable that was normally distributed for use in the General Linear Models (GLMs).

GLMs with type III hypotheses were used to quantify the relationship between support compliance, represented by ln(SS) with orangutan feeding postures, age-sex class and the other ecological and behavioural effects that may influence orangutan postural behaviours. Type III hypotheses simultaneously test the main effects alongside the interactions, allowing inclusion of both in the model (Littell et al., 2002). The modeling process began with all original variables included as main effects and all two-way interactions between age-sex class and all other variables included to further investigate the relationship between age-sex class and ln(SS). The main effects were: posture, age-sex class, support type, number of supports used for bearing weight and balance, tree zone, food type, food location, feeding method and feeding bout stage. Initially, in order to assess the relevance of supports used for balance as well as weight-bearing, both variables (i.e. supports used for weight only, and supports used for weight and balance combined) were included in the model on separate occasions to assess which was most significant. The number of supports used for both weight-bearing and balance was found to have the most significant effect and therefore was the final variable included in the model. Backwards elimination was then used to remove non-significant terms ($p = 0.05$) one at a time until only significant effects remained. More complex models could not be tested due to the relatively small sample size and large number of variables. Tukey's post-hoc tests were then used to identify which levels within a significant variable were significantly different ($p = 0.05$) with regards mean ln (SS). Confidence intervals were

calculated using one-way t-tests. All statistical analysis were performed using PASW® Statistics18.0 (SPSS Inc. Chicago, Illinois).

7.3. Results

7.3.1. GLM models

The final model is shown in Table 7.3. Of the variables tested, all were found to be significant main effects except for food type, food location, feeding method and feeding bout. The final model also contained the interaction terms age-sex*feeding method; age-sex*tree zone; age-sex*no. of supports and age-sex*feeding bout. To identify significant differences within the different variables, Tukey's post-hoc tests were performed on the main effects and interactions (see Figures 7.1 and 7.2 respectively).

Table 7.3. General Linear Model for ln(SS) as dependent variable

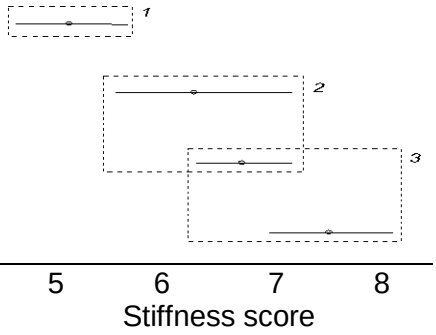
Source	Type III Sum of Squares	df[1]	Mean Square	*F*	Significance
Corrected model	171.243[2]	80	2.141	7.394	<0.001
Intercept	78.118	1	78.118	269.831	<0.001
Age-sex	3.561	3	1.187	4.100	0.007
Posture	22.159	9	2.462	8.504	<0.001
No. of supports (weight and balance)	15.668	3	5.223	18.040	<0.001
Support type	4.278	2	2.139	7.389	0.001
Tree zone	17.877	5	3.575	12.350	<0.001
Age-sex*No. of supports (BW)	5.367	8	0.671	2.317	0.018
Age-sex*Tree zone	8.533	14	0.610	2.105	0.010
Age-sex*Feed bout	5.054	8	0.632	2.182	0.027
Age-sex*Feed meth	15.698	28	0.561	1.937	0.003
Error	268.084	926	0.290		
Total	4202.571	1007			
Corrected total	439.327	1006			

[1]Degrees of freedom

[2]R squared = 0.390 (Adjusted R squared = 0.337)

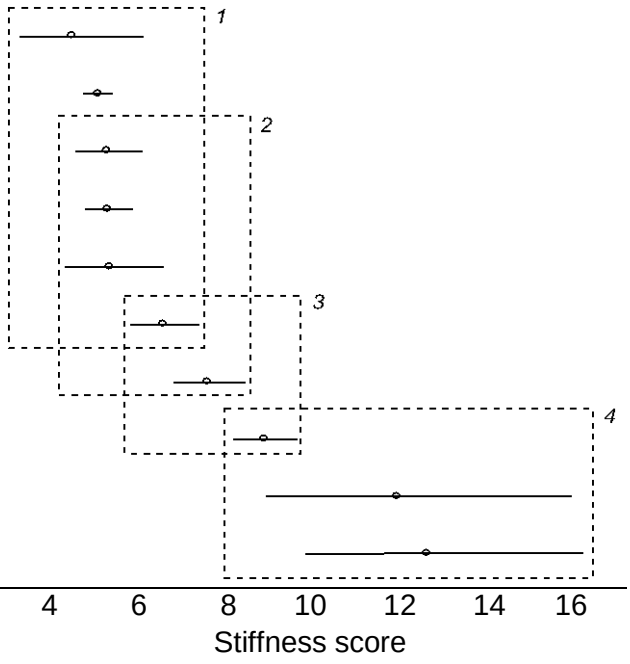
a.

Age-sex	% obs	Subset
Infants and juveniles	15.39	1
Sub-adults	13.60	2
Adult females	38.23	3
Adult males	32.77	



b.

Posture	% obs	Subset
Hindlimb suspend	1.69	1
Forelimb-hindlimb suspend	19.46	
Orthograde forelimb suspend	7.25	2
Orthograde quadrumanous suspend	10.72	
Pronograde suspend	3.57	
Squat	11.72	3
Orthograde stand	15.49	
Sit	25.62	4
Cling	1.49	
Pronograde stand	2.98	



c.

Support type	% obs	Subset
Liana	9.24	1
Mixed	7.85	1
Tree	82.92	2

5 6 7 8

Stiffness score

d.

Number of supports	% obs	Subset
Four	0.3	1
Three	27.71	2
Two	50.94	2
One	21.05	3

2 4 6 8 10

Stiffness score

e.

Tree zone	% obs	Subset
Zone 6	1.09	1
Zone 4	39.42	1
Zone 5	5.16	1
Zone 3	24.53	2
Zone 2	23.44	2
Zone 1	6.36	2

4 6 8 10

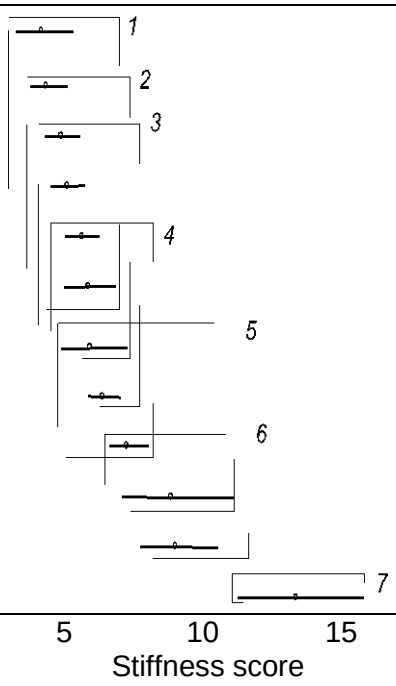
Stiffness score

Fig. 7.1. Tukey's homogenous subsets (dashed boxes) and 95% confidence intervals for mean stiffness score (cm) and a. age-sex class, b. posture, c. support type, d. number of supports

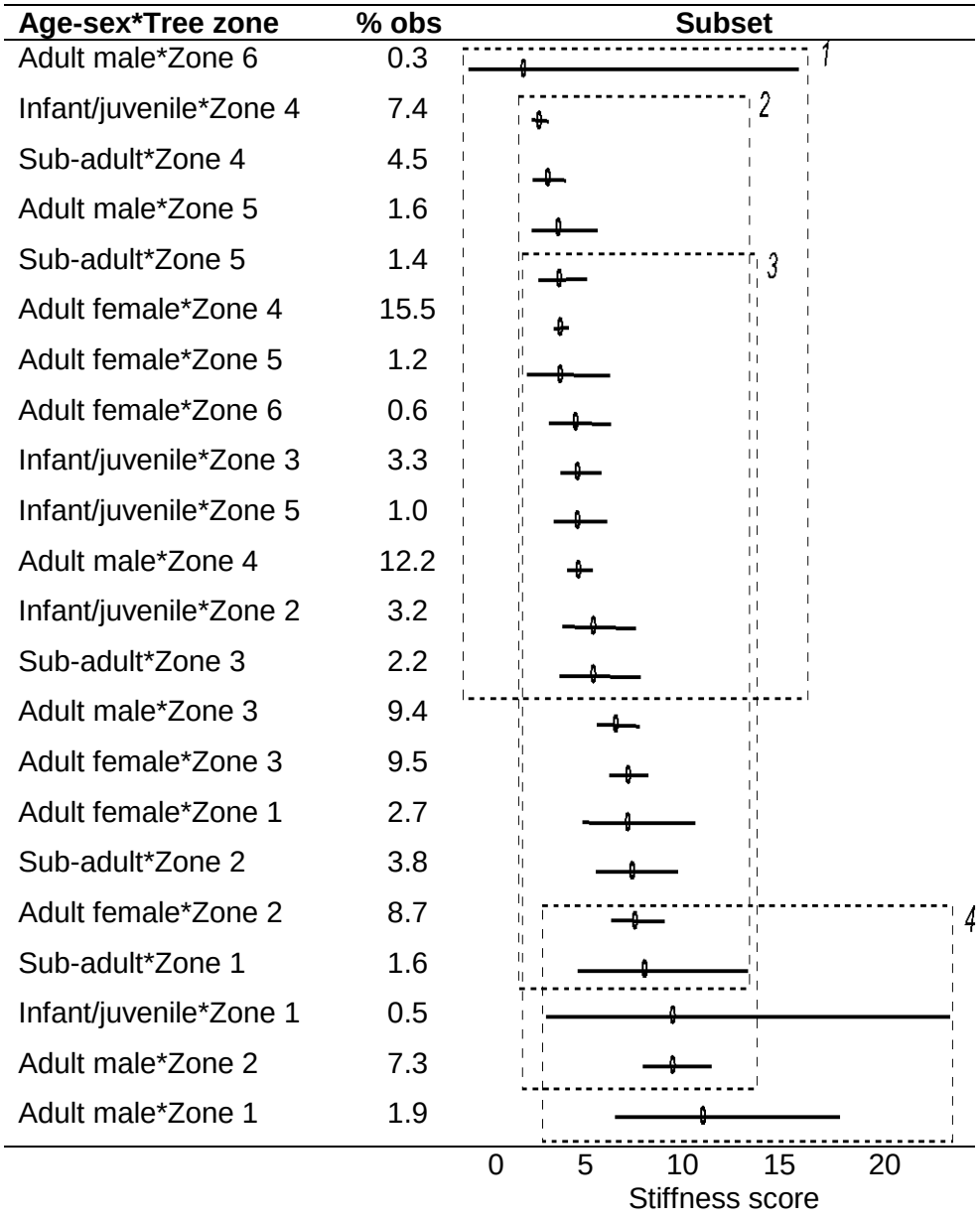
used to bear weight and for balance, e. tree zone. See Table 2 for explanation of different variable categories.

a.

Age-sex*No. of supports	% obs	Subset
Sub-adult*3	3.1	1
Infant/juvenile*3	2.8	2
Infant/juvenile*2	8.9	3
Adult male*3	10.0	
Adult female*3	11.8	4
Sub-adult*2	6.7	
Infant/juvenile*1	3.7	5
Adult female*2	18.6	
Adult male*2	16.7	6
Sub-adult*1	3.9	
Adult female*1	7.6	
Adult male*1	5.9	7

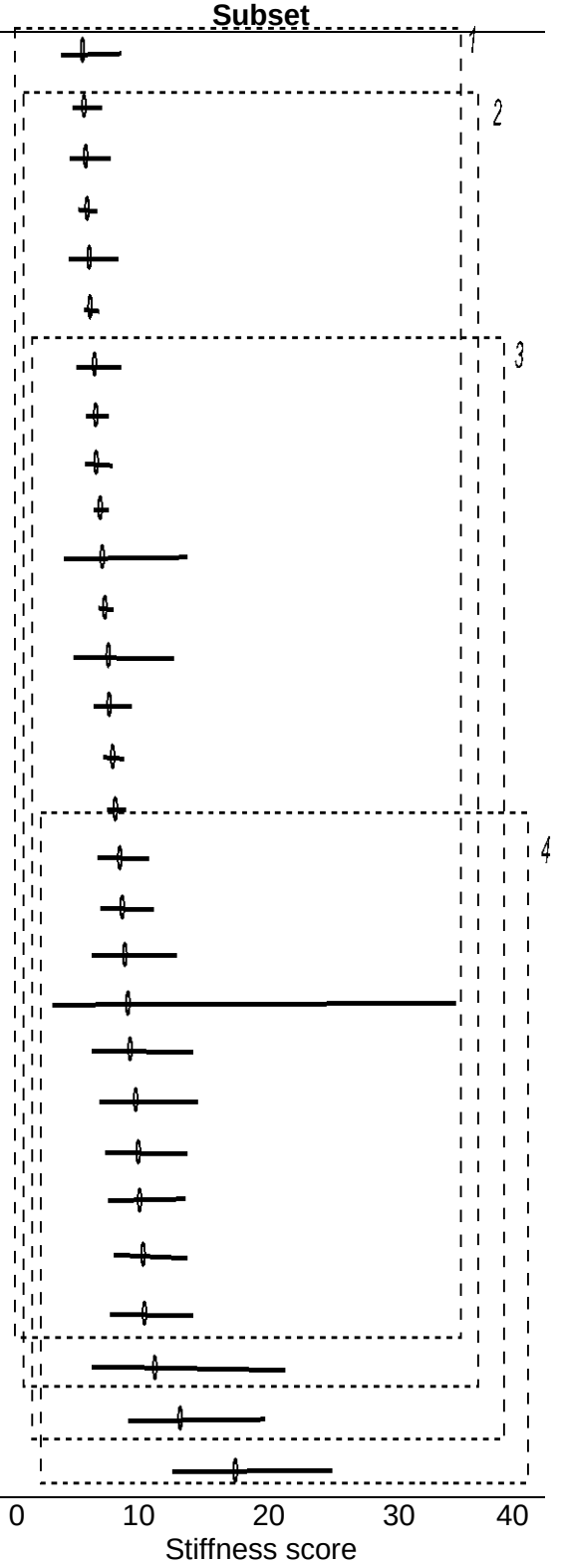


b.


Age-sex*Tree zone
% obs
Subset
Adult male*Zone 6 0.3
Infant/juvenile*Zone 4 7.4
Sub-adult*Zone 4 4.5
Adult male*Zone 5 1.6
Sub-adult*Zone 5 1.4
Adult female*Zone 4 15.5
Adult female*Zone 5 1.2
Adult female*Zone 6 0.6
Infant/juvenile*Zone 3 3.3
Infant/juvenile*Zone 5 1.0
Adult male*Zone 4 12.2
Infant/juvenile*Zone 2 3.2
Sub-adult*Zone 3 2.2
Adult male*Zone 3 9.4
Adult female*Zone 3 9.5
Adult female*Zone 1 2.7
Sub-adult*Zone 2 3.8
Adult female*Zone 2 8.7
Sub-adult*Zone 1 1.6
Infant/juvenile*Zone 1 0.5
Adult male*Zone 2 7.3
Adult male*Zone 1 1.9
1
2
3
4
0
5
10
15
20
Stiffness score

c.

Age-sex*Feed method	% obs	Subset
Infant/juvenile*Hold branch remove	0.5	1
Infant/juvenile*Attached branch mouth	2.7	2
Infant/juvenile*Insects (leaves)	0.7	
Sub-adults*Attached branch mouth	3.6	
Infant/juvenile*Bark (limbs)	0.7	
Infant/juvenile*Attached branch remove	7.5	
Sub-adult*Bark (limbs)	1.0	3
Adult female*Broken branch mouth	3.6	
Infant/juvenile*Broken branch mouth	2.7	
Adult female*Attached branch remove	15.4	
Sub-adult*Insects (limbs)	1.0	
Adult female*Attached branch mouth	11.3	
Sub-adult*Insects (leaves)	1.0	
Sub-adults*Attached branch remove	4.4	
Adult male*Attached branch mouth	11.0	
Adult male*Attached branch remove	14.2	
Sub-adult*Broken branch mouth	1.6	4
Adult male*Broken branch mouth	2.1	
Adult male*Bark (limbs)	1.2	
Infant/juvenile*Insects (limbs)	0.5	
Adult male*Insects (limbs)	1.2	
Adult male*Hold branch remove	1.2	
Sub-adult*Bark (mouth)	0.8	
Adult female*Insects (leaves)	1.9	
Adult female*Insects (limbs)	2.6	
Adult female*Bark (limbs)	1.8	
Adult female*Hold branch remove	0.6	
Adult male*Insects (leaves)	1.9	
Adult female*Bark (mouth)	1.1	



d.

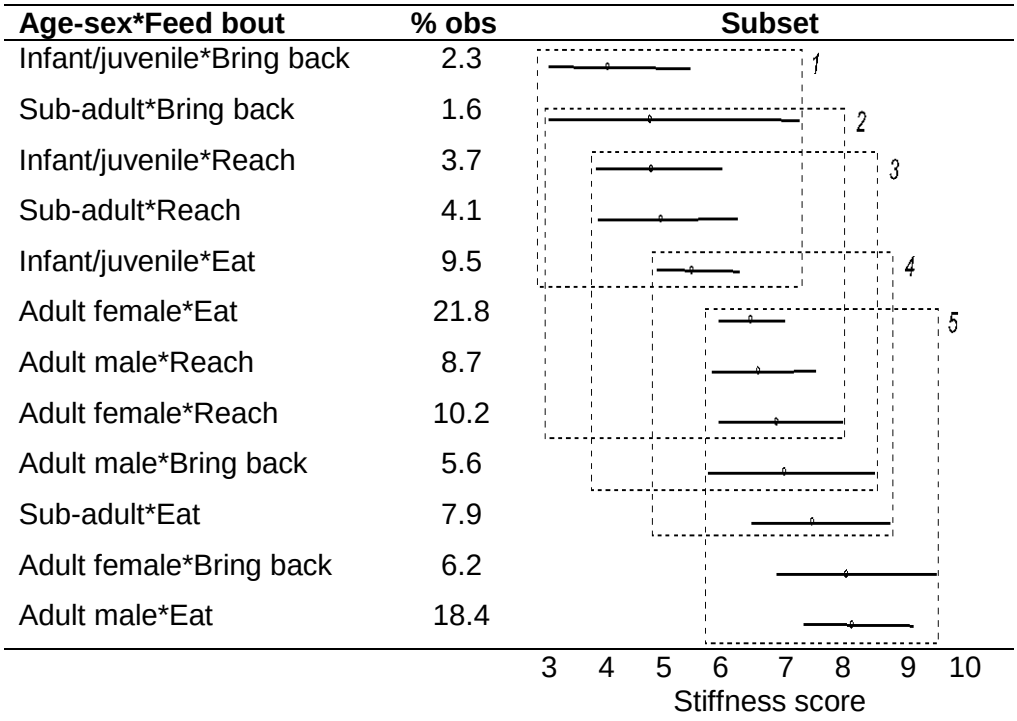


Fig. 7.2. Tukey's homogeneous subsets (dashed boxes) and 95% confidence intervals for mean stiffness score (cm) and the interactions. Interactions are significantly different when they do not appear in the same subset. a. age-sex class*no. of supports (adult males, adult females and sub-adults were only observed using four supports once, and thus are not included in the figure as no confidence intervals are available. Infants and juveniles were never observed using four supports.), b. age-sex class*tree zone; sub-adults in tree zone 6 not included as only observed twice; mean SS: 4.57 cm), c. age-sex class*feeding method (infant/juvenile*bark (mouth); sub-adults*hold branch remove and adult male*bark (mouth) not included as observed only once), d. age-sex class*feeding bout.

The results show that infants and juveniles used significantly more flexible mean supports than sub-adults, adult females and adult males (Fig. 7.1a). Sub-adults also used supports with

a significantly lower SS than adult males, but they did not differ significantly from adult females. Figure 7.1b shows the relationship between posture and support stiffness, and reveals that, overall, suspensory postures occurred on supports of lower stiffness than compressive postures. Specifically, hindlimb suspend and forelimb-hindlimb suspend were used on supports with a significantly lower SS than orthograde stand, sit, cling and pronograde stand. In contrast pronograde stand and cling were used on stiffer supports than all other postures, except for sit.

Orangutans were able to utilise supports with lower stiffness scores when they used lianas and a mixture of trees and lianas than when they used trees exclusively (Fig. 7.1c). As the number of supports used increased, the mean stiffness score decreased from 9.78 cm (one support) to 3.12 cm (four supports; Fig. 7.1d). The mean SS was significantly greater when one support was used and significantly less when four supports were used (although note the large confidence interval for this category) compared to the use of two and three supports. Finally, tree zone was divided into two significantly different subsets (Fig. 7.1e), with tree trunks, major and intermediate branches (zones 1-3) being associated with stiffer supports than terminal branches (zone 4), lianas between zones (zone 5) and postural bouts that spanned across all zones (zone 6).

Tukey's results for the significant interactions are presented in Figure 7.2. Figure 7.2a shows that overall, multiple supports enabled all age-sex classes to use supports with a lower mean SS. Furthermore, with the exception of infants and juveniles, the use of single supports seems to restrict orangutans to relatively high stiffness scores, particularly adult males who used

single supports with a significantly greater mean SS than any other age-sex class. Fig. 2b shows that the mean values for stiffness score across all age-sex classes in all tree zones were very close to one another and the confidence intervals were relatively large for both the lowest and highest stiffness scores. However, overall, accessing tree zones 4, 5, and 6, which consists of the terminal branch niche, lianas between trees and postures that span all zones, allowed all orangutans to utilise the smallest supports. The most notable result from this graph is that adult males were able to use supports of lower mean SS than all other age-sex groups by using supports across all zones within a tree, although the confidence interval is very large.

Although none of the feeding behaviour variables were significant main effects in the final model, feeding method and feeding bout stage interacted with age-sex class significantly. Figure 7.2c shows that infants and juveniles used supports with significantly lower stiffness scores (they do not appear in the same subset) when feeding by holding the branch with one limb and removing food items with another limb (a method used to feed on both fruit and leaves), compared to adult females using the same feeding method, and also adult females removing bark using the mouth, and adult males feeding on insects from leaves. In general the stiffest mean supports were most frequently used by adult females feeding on bark using both the mouth and limbs, insects using leaves and limbs and when holding a food branch and removing individual items. Adult males eating, and adult females bringing back a food item (Fig. 2d) were used on significantly stiffer supports than sub-adults reaching for, or bringing back a food item and infants and juveniles at any bout stage (eating, reaching or bringing back). Infants and juveniles, together with sub-adults used supports of significantly lower SS when bringing back a food item compared to adult males and adult females bringing back, and adult females eating.

7.4 Discussion

7.4.1 The use of suspensory postures during feeding in the terminal branch niche

Morphological adaptations for orthogrady are considered to be the uniting features of the great apes (see Pilbeam, 1996; Crompton et al., 2008). Orthograde suspensory behaviours, in particular, are considered to be an important adaptation for feeding and moving on smaller branches, such as those found in the terminal branch niche (e.g. Grand, 1972; Cartmill, 1985; Hunt, 1996; Pilbeam, 1996; Larson, 1998; Crompton et al., 2008). The results of the present study confirm both the location of the smallest supports in the terminal branch niche (zone 4), and that this was the most important feeding zone (40% of all observations), which likely relates to the fact that the majority of nutritionally beneficial foods are found here (Houle et al., 2007). The use of suspensory postures during feeding was also associated with the more compliant supports, with the five suspensory postures being employed on supports of lower mean stiffness score than the five compressive postures recorded in this study. However, contrary to the predictions that the great apes are characterised by orthogrady as an adaptation for terminal branch niche feeding (see Hunt 1991, 1996), the suspensory postures used by orangutans included both orthograde and pronograde torso orientations. Hindlimb suspend (orthograde) and forelimb-hindlimb suspend (pronograde) were the postures used on the most compliant supports. Whereas as hindlimb suspend was employed infrequently, forelimb-hindlimb suspend was the second-most commonly used posture (19.5% of observations) and had a very small confidence interval. It therefore appears to be selected by orangutans specifically for use on very small supports.

Forelimb-hindlimb suspend involves suspension, generally from one forelimb and one hindlimb (although both hindlimbs can be employed), with the torso on its side in a pronograde orientation (Hunt et al., 1996; Thorpe and Crompton, 2006). During feeding, the free forelimb is most frequently used to reach and obtain the food. The other non-human apes have rarely been observed using such a posture (see Hunt, 1991, 1992a, b; Doran, 1993a, b; Fleagle, 1999), although the positional behaviour of bonobos, gorillas and gibbons is poorly characterized, which renders comparison difficult. Chimpanzees, bonobos and gibbons usually feed in the TBN using unimanual orthograde arm-hanging modes (Hunt, 1992a; Fleagle, 1999), whereas, although gorillas enter the TBN using orthograde suspensory behaviours, they usually sit or squat when foraging (Remis, 1995). Forelimb-hindlimb suspend confers the same benefits as unimanual orthograde suspend in that it increases safety via suspension (Cartmill, 1985), and extends foraging radius (Grand, 1972), but by using multiple limbs for weight bearing and balance, it enables body mass to be distributed between multiple supports. This reduces the risk of falling if one support should break and also reduces the stress placed on each limb (see Thorpe and Crompton, 2006), while still leaving a forelimb free to reach for food items.

The importance of forelimb-hindlimb suspend agrees with the results for orangutan locomotion, where pronograde bridge and pronograde suspensory locomotion using multiple supports enabled movement on smaller supports than did exclusively orthograde behaviours (Thorpe et al., 2009). However, in the present study pronograde suspend, while part of the same subset as forelimb-hindlimb suspend, was used, on average, on stiffer supports than orthograde quadrumanous suspend and was also used infrequently during feeding (3.57%). Its lack of use during feeding is most likely because it requires at least three limbs to be in

suspension, with the torso facing up or down, a position not conducive to reaching over a wide area for food. Rather, forelimb-hindlimb suspend may be the postural alternative to pronograde suspend that enables the use of the smallest supports during feeding in the TBN.

Overall, the results lead to the acceptance of both our first and second hypotheses; that suspensory behaviours will play a specific role during feeding, and that they will be used on the more compliant supports, although they counter the suggestion that it is orthograde postures that facilitate great ape feeding in the terminal branch niche. While orangutans do utilise unimanual orthograde forelimb suspend for feeding, it was not observed as frequently (7.3% of observations). This is likely to be related to the increased risk of placing all body weight on one support compared to the other modes available to orangutans. Instead, orangutans show further specific adaptations to their arboreal habitat in the form of forelimb-hindlimb pronograde suspension that provides a more successful and risk free TBN feeding strategy. This supports our third hypothesis that pronograde suspension will play a specific role during feeding on compliant supports. The use of these behaviours by orangutans and not the other great apes (see Hunt, 1991, 1992a, b; Doran, 1993a, b; Fleagle, 1999), despite their benefits when feeding in the TBN, implies that they evolved in orangutans after their separation from the common great ape ancestor as a specialization to their predominantly arboreal lifestyle, as has previously been hypothesized for the use of pronograde suspensory locomotor modes in orangutans (Thorpe et al., 2009). The lack of adaptation to forms of pronograde suspension (including forelimb-hindlimb suspend) in the African apes possibly reflects their need to be additionally adapted for terrestrial locomotion, which must conflict with adaptations for pronograde suspension when arboreal (see Thorpe et al., 2009).

7.4.2 Age-sex differences in positional behaviour and habitat use during feeding

We further hypothesised that there would be an age-sex class difference in the use of either suspensory postures or in the use of the habitat itself (Cartmill and Milton, 1977; Cartmill, 1985; Cant, 1987a, 1992). However, age-sex class and posture did not interact to have a significant association with support stiffness, countering the expectation that adult males would show greater association with suspensory postures on smaller supports than other age-sex classes. This is similar to the observations of Thorpe and Crompton (2005) whereby there were no differences in locomotor behaviour between the different age-sex classes of orangutans. They related the lack of age-sex differences in suspensory locomotion to the use of the same arboreal pathways by the different age-sex classes (Thorpe and Crompton, 2005). Here we propose that similarity in feeding postures may be related to the safety benefits provided by the different behaviours. The same postures would enable individuals of all age-sex classes to use smaller supports relative to their body mass, than unimanual postures, therefore enabling them to access the TBN more effectively.

We did, however, find support for the expectation that the different age-sex classes would use their habitat differently, agreeing with the predictions of Grand (1972, 1984) and Ripley (1979) and the observations of gorillas (adult females used smaller supports than adult males during feeding; Remis, 1995) and orangutans (support size increased as the weight class of orangutans increased i.e. from infants to flanged adult males during postural feeding behaviours; Cant, 1992). The use of larger mean supports by adult males in the present study is likely to be related to safety, as the stiffer supports can bear larger masses, thus reducing the risk of falling (Cartmill and Milton, 1977; Cant, 1992, 1994). Remis (1995), however, also

found that along with using more compliant supports than male gorillas, female gorillas used the terminal branch niche more, but this relationship was not found in the present study since adult males and females fed in Zone 4 for 12% and 15.5% of their time respectively. Rather, adult male orangutans used all trees zones, including the TBN, with a similar frequency to the other age-sex classes, but when using the trunk, major branches and terminal branches adult males tended to use stiffer supports. This implies that adult males specifically select the larger branches for use in these zones where possible, whereas the smaller individuals are able to use a wider range of support stiffness. This may also be related to the prevalence of large fruiting fig trees at Ketambe (see Rijksen, 1978; Thorpe and Crompton, 2005), which, due to their large size, enable adult males to access the TBN using relatively large supports.

Interestingly, adult males also used supports with the lowest mean stiffness of any age-sex class when positioned across all tree zones and when using lianas between trees. This may be related to the properties of the supports in these instances. Trees in which all zones can be used at once will be smaller (as the animal must be able to reach across all zones) and thus, by default, all the supports used will be smaller. When using all zones, by using the stronger trunk or a main bough to bear some of the body weight, adult males may be able to use these smaller supports. Furthermore, as lianas often hang vertically through the canopy, body mass is often applied along the line of action of the liana. This reduces the chance of it breaking relative to the amount of mass applied (see Thorpe et al, 2009), which seems to offer an important opportunity for animals of larger body mass to exploit key feeding zones.

7.4.3 The relationship between foraging behaviour, support stiffness and age-sex class

None of the foraging behaviour variables included in this study (food type, food location, feeding method or feeding bout stage) were directly related to the stiffness of supports used during feeding in orangutans. However, age-sex class did form significant interactions with feeding method and feeding bout stage, partially supporting hypothesis five, that differences in feeding behaviour will influence the compliance of the supports used in combination with the postures observed and age-sex class due to the different physical abilities required to obtain different foods. By its nature, feeding method can inform us about the types of food eaten, as the methods 'attached branch to mouth', 'broken branch to mouth', 'attached branch remove' and 'hold branch remove' were used to feed on fruit and leaves, whereas the remaining methods were used to feed on bark and insects (as indicated by their names). The use of supports with significantly greater mean stiffness when feeding on bark (mouth) by the adult females, and insects (leaves) by the adult males in comparison to infants/juveniles feeding using hold branch remove, is likely related to the location of these food types. Bark is most frequently stripped from either the trunk or major branches, using compressive postures (Thorpe and Crompton, 2006; Myatt, pers. obs) and requires a reasonable amount of force to remove the bark. Therefore, such methods are more likely to require a stiffer, more stable base. The method insects (leaves) generally involved the removal of bundles of vegetation from mats of epiphtyes, which were more often located on the major tree branches. Furthermore as feeding on one bundle of leaves took a relatively long period of time, individuals would often choose to move to a stable branch to sit and eat this food type, which would increase its association with stiffer supports.

Infants, juveniles and subadults, however, fed using insects (leaves) and bark (limbs) on the most compliant supports. This difference may be related to the fact that infants and juveniles often fed on bark and insects (leaves) taken from their mothers. These are particularly hard food items to process and mothers often allow their offspring to take these food items until they are eight years old (see van Noordwijk et al., 2009). Infants and juveniles would often use hindlimb suspend on the most compliant supports to feed and play with these foods, possibly to place themselves out of easy reach of other orangutans that may try to steal the food. The continued use of compliant supports in association with these feeding methods in sub-adults may suggest that they are still developing adult-like competence in locating and processing these more difficult to find food items (van Noordwijk et al., 2009).

Age-sex class and feeding bout stage were related to mean support stiffness in that infants and juveniles were able to both reach, bring back and feed all on the smallest supports, probably due to the reduced risk of being located on compliant supports for a longer period of time for smaller individuals. Adult males, however, would use more compliant supports when reaching or bringing back a food item, but would eat on stiffer supports (also see Thorpe and Crompton, 2009). This pattern of eating on stiffer supports than were used for obtaining the food was also observed in the sub-adults, although overall they used smaller supports than adult males. This relationship is likely related to safety as an individual may risk more to retrieve a food item, but choose to move to a more secure location to feed for a longer period of time. Adult females, however, did not follow this pattern; rather they actually ate on supports of slightly lower mean stiffness than they used to reach/bring back the food. As all of the adult females in this study had dependent offspring, this may be related to their desire to stay close to their infants (who were using more compliant supports for all stages) in case of

any problems (van Noordwijk et al., 2009). This is in contrast to the more conservative nature of adult females observed during locomotion (Thorpe et al., 2009), but further reflects a strong link between social behavior and positional behaviour for adult females.

7.4.4 Concluding remarks

Overall, this study has shown that, in agreement with previous studies suspensory behaviours were the best solution for using the small supports found in the TBN. However, it was not the use of orthograde suspensory behaviours, as expected, but the use of pronograde suspensory postures, such as forelimb-hindlimb suspend, that were used during feeding on the most compliant supports. These postures may enable orangutans to exploit the terminal branch niche with greater efficiency and safety by distributing body weight and using limbs for balance across multiple supports. Such behaviour is likely to reflect the refinement of arboreal habitat use in orangutans since their split from the last common ape ancestor. Age-sex related differences appear to highlight the fact that although adult males, with their larger body mass, are capable of exploiting the same niches as the smaller individuals, they may take less risks to do so, by employing stiffer supports and only using the smallest supports when strictly necessary i.e. to obtain the food. Furthermore, adult females appear to alter aspects of their feeding behaviour in response to the needs of their offspring, indicating that social factors may also play a role in behaviour and habitat use. Overall, this study, has shown how orangutans have become successful at feeding in the TBN to gain the greatest nutritional benefit, despite their large body mass and the complex habitat in which they live. It further shows that feeding postures may be important selective factors in the development of new positional behaviours.

CHAPTER 8

GENERAL DISCUSSION

8.1. Discussion

By identifying the relationships between morphology and behaviour in the non-human apes, and establishing the response of these features to the selective demands of the environment, we were able to more effectively investigate the evolution of diversity within this group and our understanding of the influences and constraints acting upon them. The primary objectives of this thesis were to undertake a comprehensive comparison of non-human ape morphology, and combine this knowledge with a detailed understanding of the behaviours used by orangutans in their complex arboreal habitat. The principle research aims stated in Chapter 1 have been met and, as such, our understanding of the morphology-behaviour-habitat interface in the non-human apes, particularly in the arboreal specialist, the orangutan, has been expanded. In particular, the development of new methods to record and analyse anatomical and behavioural data has enabled a deeper understanding of the more subtle adaptations that reflect the morphological and ecological diversification in these, our closest living relatives.

8.1.1. Shared macro-architecture, specialised micro-architecture

In chapters 2 and 3 macro-architecture properties of the fore and hindlimbs in the non-human apes were compared using both scaling techniques and statistical analysis. Data obtained in this study significantly added to the overall dataset of non-human ape muscle architecture, including the first data from bonobo and gorilla forelimbs, thus providing a larger dataset for comparison. Species comparisons were performed using both allometric scaling, establishing specific scaling exponents for individual muscle groups and general linear models to take into account the large differences in body mass between the different species that would obscure any differences due to variations in locomotor behaviour. Both methods had advantages and

disadvantages, although general linear models would provide the more robust comparison if a larger dataset were available, and thus increasing the number of data available from all species, and all age-sex classes should be a top priority in future studies.

From both methods of analysis, although some significant differences were highlighted e.g. chimpanzees and orangutans differed in the PCSA of their gluteal muscles, overall, we found that the non-human apes did not vary significantly in the majority of muscle groups from either the fore or hindlimb. This contradicts previous expectations and results from studies of non-human muscle architecture, that even small differences in the frequencies of locomotor behaviour use and/or predominant habitat use will be reflected in their macro-architecture (e.g. Fleagle, 1977; Fleagle and Meldrum, 1988; Ward and Sussman, 1979; Payne et al., 2006a; Oishi et al., 2008, 2009; Channon et al., 2009).

The difference between the result in chapters 2 and 3 and previous studies is most likely due to the different methods used to assess the data. Previous studies often used geometric scaling (e.g. Thorpe et al., 1999; Payne et al., 2006a; Channon et al., 2009) which, as discussed in chapter 2, is likely to introduce error and bias into the data (Packard and Boardman, 1987, 1999). The present study (chapters 2 and 3) was the first to statistically analyse the variation between the non-human ape species, rather than using personal judgment to visually assess the differences present, although this does raise questions as to whether a statistically significant differences is the same as a functionally significant difference. However, due to the inconsistencies that can arise regarding the scale of a difference depending on the scaling exponent used (demonstrated in chapter 2), at this time it may be more appropriate to use

statistical analysis as the basis for the conclusions. This study therefore, has not only highlighted a crucial problem with the analysis of anatomical data that can influence the conclusions reached, but has also provided an alternative, more appropriate method to employ in future studies.

Overall, the Asian apes (gibbons and orangutans) appear to be no more adapted to their arboreal habitat than the African apes (chimpanzees, bonobos and gorillas) based on their macro-architecture (chapters 2 and 3), rather, it appears, that if a behaviour is performed at all, muscles will need to be adapted to perform that function, and a muscle will never develop capabilities beyond those necessary (Alexander et al, 1981). In the non-human apes this likely reflects more clearly that they are characterised as a group by orthograde behaviours and that their locomotor repertoires overlap greatly (Thorpe and Crompton, 2006). Furthermore, this highlights that even though they differ in terms of the frequency of different behaviours, and even the kinematics of different behaviours e.g. vertical climbing differs between the Asian and African apes (Isler, 2005), evolutionarily, they share a very close history (Crompton et al., 2008) and the specialisations developed since the split from the last common ape ancestor may be more subtle.

The results from chapter 4, assessing the variation in fibre type distribution between chimpanzees and orangutans support this finding from the macro-architecture, as differences were apparent in this plastic and more readily adaptable feature of muscle architecture, likely associated with differences in locomotor behaviours and habitat use. Orangutans were characterised by a significantly greater proportion of slow fibres in all three muscles of the

triceps surae, compared to chimpanzees, and the chimpanzees had an unusually high proportion of fast fibres in their soleus muscle compared to other mammals (e.g. Edstrom and Nystrom, 1969; Gollnick, 1974; Edgerton, 1975; Dahmane et al., 2005). Orangutans are more likely to need slow fibres for their use of slow, controlled locomotor behaviours, which are adaptations to the arboreal habitat and the need to control for the effects of support compliance (Thorpe and Crompton, 2005, 2006; Thorpe et al., 2009; also see chapter 1). The regionalisation of fast fibres in orangutan triceps surae muscles possibly reflects their use of dynamic stabilisation, as by being able to undertake quick, correctional movements, orangutans are able to more effectively control their balance. Balance control strategies are important in arboreal habitats, particularly for large-bodied primates such as orangutans, as during multiple support use, subtle adjustments in the positioning of the different limbs enables them to control the effects of support compliance and maintain stability to reduce the risk of falling, as was found during feeding in the terminal branch niche (chapter 7).

The increased proportion of fast fibres in chimpanzee soleus muscle in comparison to other mammals was proposed to be an important mechanism by which chimpanzees are able to increase their acceleration and power when terrestrial (needed during social conflict); but without compromising their ability to produce forces over a greater range of motion when arboreal, as reflected by their macro-architecture (long muscle fascicles and smaller PCSAs; chapter 2). This study highlights the importance of studying anatomy at the micro-architecture level in addition to gross anatomy, as this is where more subtle adaptations to the specific locomotor needs of a species may be found. As this was the first study to measure the fibre type distribution in the limb muscles of non-human apes it has highlighted the importance of

this additional parameter when relating morphology to behaviour in any species and opened the doorway to a new body of research in the non-human apes.

8.1.2. Orangutans, the arboreal specialists

To further understand how an environment, such as the complex arboreal habitat, might influence the behaviours and morphology in the non-human apes, a field study of orangutan positional behaviour was undertaken, as due to their predominantly arboreal lifestyle and large body mass they are most likely to have evolved specific adaptations to this niche (Thorpe et al., 2009; Crompton et al., 2008). In order to assess the variation within positional behaviours at a more detailed level, a new method was developed based on Sutton Movement Writing (SMW; Chapter 5). This method enabled collection of both locomotor and postural data with relative ease in the field and has thus enabled a more specific analysis of aspects of orangutan positional behaviour including specific limb positions and all aspects of support use i.e. for both weight-bearing and balance. Although SMW would not be appropriate for recording very fast forms of locomotion and reduces the ability to obtain large sample sizes, it enabled the more detailed recording of the variation within oscillatory behaviours and feeding specialisations used by orangutans (chapters 6 and 7 respectively).The development of this method for use in primates has contributed an alternative method which could be adapted and used with any primate species, indeed, any animal, where there was a desire to focus on the specific spatial arrangement of limbs, or the use of a complex habitat in situations where video recording is not a practical option.

Sutton Movement Writing was employed in chapter 6 to record the variation, not previously recorded, within oscillatory behaviours in orangutans and to classify the postures observed in a quantitative manner. This study (chapter 6) also provided the first quantitative classification of positional behaviours using clustering analysis. While this method has a number of limitations e.g. only data reflecting a static posture can be used as input traits, it may provide a method by which the complexity within positional behaviours can be quantified, something which has yet to be achieved. Oscillatory behaviours are crucial in enabling orangutans to effectively navigate through the forest canopy (e.g. Cant, 1994; Thorpe and Crompton, 2005, 2006; Thorpe et al., 2007a) and the postures maintained most frequently during these behaviours were orthograde and pronograde suspension. This re-iterates the importance of suspension in an arboreal habitat as a mechanism against falling (Grand, 1972; Cant, 1992, 1994; Povinelli and Cant, 1995). The frequent use of pronograde suspension observed during these behaviours further emphasises the key role of this behaviour, unique to orangutans, in all aspects of arboreal habitat use (also see Thorpe et al., 2009; chapter 7).

The role of pronograde suspension in the positional behaviour repertoire of orangutans was once again highlighted as a key adaptation to their arboreal habitat in chapter 7. Together with multiple-limb orthograde suspension (i.e. orthograde quadrumanous suspend), these multiple support using postures appear to be a particular specialisation for feeding in the terminal branch niche. Multiple support use confers significant benefits for stability and safety in an arboreal habitat, particularly in large-bodied primates, where supports will be more likely to break beneath their mass and the dangers of falling are increased (Cartmill, 1985; Cartmill and Milton, 1985). The development of such specific behavioural adaptations to the arboreal habitat in orangutans likely further reflects the refinement of their arboreal behaviours since

their split from the last common ape ancestor (see Thorpe et al., 2009). This study has therefore provided further evidence to emphasise the crucial role of this unique behaviour to the success of orangutans.

8.1.3. Form and function relationships in the non-human apes

Understanding form and function relationships, such as those between morphology and the behaviours performed in an extant species, can inform us about the adaptations undergone since the split from the last common ape ancestor. This study has shown that, unexpectedly, despite the differences in lifestyle and the frequencies with which the different positional behaviours are used in the non-human apes, their macro-morphology remains remarkably similar (chapters 2 and 3). This likely reflects the fact that overall they still utilise a very similar suite of behaviours, albeit to different degrees and their muscles will need to be able to produce the forces necessary to undertake these movements, however rare (Preuschoft, 1967). The key behavioural difference highlighted in this study as a specialisation for moving a large body mass on compliant arboreal supports, was the use of pronograde suspension by orangutans (chapters 6 and 7). This has been previously highlighted as important during locomotion (Thorpe et al., 2009) and has now been shown to be a critical behaviour by which orangutans feed in the terminal branch niche (chapter 7), and plays a role during gap crossing behaviours (chapter 6). This behaviour appears to have evolved in orangutans since their split from the last common ancestor of the non-human apes (Thorpe et al., 2009), and has increased their fitness in the complex arboreal habitat.

While adaptations to this behaviour were not explicitly identified within their macro-architecture, due to the muscle group studied, they may be present in the micro-architecture. Chapter 4 highlighted the fact that while variations may be absent in the gross anatomy, differences related to the use of different behaviours and the influence of the habitat can result in different proportions of muscle fibre types. Therefore, further adaptations to the behaviours key to the success of the different non-human ape species may be apparent at this level. Overall, this study has uncovered some of the more subtle ways in which species can be tailored to the specific requirements of their habitat and lifestyle and further highlights the importance of their environment in shaping alternative behaviours. In particular, the complex, arboreal habitat has resulted in behaviours not found within the repertoire of the other apes, which indicates that the selective pressures of such an environment are likely to be extremely high, due to the risks involved, such as falling. This study, therefore, has contributed to our understanding of the evolution of diversity in the hominoids, and the specialisations undergone by the largest, predominantly arboreal primate, the orangutan, in relation to the complexity of their forest habitat and their use of compliant supports. As the number of orangutans remaining in the wild becomes ever smaller due to the destruction of their habitat, these studies increase in importance. A detailed understanding of the relationship with the habitat in this, our last predominantly arboreal ancestor, will not only assist in the understanding of our own evolution, but will play an important role in the conservation of this species for years to come.

8.2 Ideas and recommendations for future studies

The development of new methods to both record and analyse the data obtained was a crucial aspect of this study and has provided scope for future studies to further develop our understanding of the morphology-behaviour-habitat interface in a range of species. Overall, however, the studies of macro- and micro-architecture (chapters 2, 3 and 4) would benefit from increased sample sizes. This would be particularly beneficial for the fibre typing study (chapter 4) as data were only available from two chimpanzees and one orangutan. Increasing the sample size, however, can be problematic as it requires fixed cadavers, preferably ones that have not been frozen and defrosted multiple times prior to fixation. The low availability of non-human ape cadavers and the additional need for fresh cadavers for studies of macro-architecture places a high demand on what is a poorly available resource. Future studies, however, should aim to increase the sample size of all species to enable further comparison in relation to their positional behaviours and habitat.

Future micro-architecture work that would be particularly interesting would include a study of the triceps surae in gibbons, due to the presence of a well-developed Achilles' tendon in this species (Vereecke, 2006). Humans and gibbons are the only apes to have substantial Achilles' tendons, the remaining apes usually have a small, insignificant Achilles' tendon (Swindler and Wood, 1973; chapter 4, pers. obs). Gibbon locomotion is characterised by bouts of brachiation with short periods of arboreal bipedalism with a 'bouncing' gait along relatively stiff, horizontal boughs (Fleagle, 1999; Vereecke et al., 2006a) and therefore the Achilles' tendon would appear to be an ideal candidate for storing and returning elastic energy during this behaviour. However, Vereecke et al. (2006a) found that the kinematics of the gibbon

ankle-joint during bipedalism did not support this, although measures of the stress-strain properties of the tendon itself do support its role in increasing energetic efficiency during locomotion (Vereecke et al., 2008). Thus a question remains regarding the role of the longer Achilles' tendon during gibbon locomotion. Investigating the distribution of the muscle fibre types in the triceps surae of gibbons, therefore, may shed light on the functional adaptations present in the micro-architecture in relation to the overall muscle architecture and how this relates to the presence or absence of an Achilles tendon in relation to their positional behaviour.

Studies of other muscle groups would also be of interest, particularly those highlighted as possibly playing a role during the unique locomotor behaviours observed in the different non-human ape species e.g. pronograde suspension in orangutans (Thorpe et al., 2009; chapter 7). These behaviours have been identified as enabling the use of more compliant supports both during locomotion (Thorpe et al., 2009) and feeding (Chapter 7) and appear have developed in orangutans as an adaptation to their predominantly arboreal lifestyle (Thorpe et al., 2009; chapters 6 and 7). The forelimbs of all non-human apes are adapted for suspension (Larson, 1998; Ward, 2007), however, as the other non-human apes do not appear to use pronograde suspensory modes their hindlimbs are used less for suspension (e.g. Hunt et al., 1992a, b; Doran, 1993a, b; Remis, 1995; Fleagle, 1999; Thorpe and Crompton, 2005, 2006; Thorpe et al., 2009).

Therefore, one might expect adaptations in the hip and thigh musculature of *Pongo* in comparison to those of *Pan* and *Gorilla*, as the function of these muscles and the stresses

experienced during pronograde suspension are likely to differ to those undergone during quadrupedal walking, for example. A significant difference in the PCSA of the gluteal muscles between chimpanzees and orangutans was evident from chapter 2, with chimpanzees adapted for greater maximum force production (larger PCSA) compared to orangutans that were adapted for greater mobility (also see Payne et al., 2006a). This may be related to the use of pronograde suspensory behaviours by orangutans, requiring the ability to produce force both in compressive and suspensory positions. Differences in the function of the gluteal muscles between these two species have also been identified during quadrupedalism (Stern and Susman, 1981), possibly reflecting the specialisations present in chimpanzees for terrestrial quadrupedalism that restrict their ability to use pronograde suspension in the canopy. Further differences are therefore expected in the fibre type profile of these muscles. A key aim of future studies of morphological adaptations in the non-human apes should also be to undertake studies of muscle fibre type distribution in other muscle groups that may also show specific adaptations to the different lifestyles in the non-human apes, as identified from studies of positional behaviour. This would provide a more detailed analysis of the morphological diversity present in order to further understand how this is reflected in the variations present in behaviour and habitat use.

The SMW method developed in chapter 5 provides scope for a wide range of studies investigating in detail the relationships between positional behaviour and habitat use in a range of species. Although, the cluster analysis method employed in chapter 6 would need refining before the use of supports and other behavioural variables could also be incorporated, this method does appear to provide a possible technique to enable such detailed comparisons. With regards oscillatory behaviours, a larger data set would enable the relationships between

posture, support use, gap crossing context (e.g. gap size) and age-sex class to be quantified. In particular, their use of pronograde suspensory postures during these modes would be interesting, to see if they enable the crossing of larger gaps, for example, thus further demonstrating their role as a specific adaptation to life in the forest canopy. A detailed comparative study of the use of tree sway in orangutans compared to the other non-human apes observed using them (*Pan*: Doran, 1993a, b, 1996; *Gorilla*: Remis, 1995) may also shed light on any specialisations within these behaviours that may distinguish their use in the different species.

Finally, SMW and cluster analysis could also be used to provide a more detailed understanding of changes in positional behaviour during ontogeny; laterality of different behaviours and differences in the positional behaviour of morphologically similar species living in different habitats or differences in the way in which morphologically distinct species exhibit the same behaviours (according to standardized classification systems). In orangutans, it would be particularly interesting to compare how both the different species (i.e. Bornean and Sumatran orangutans) perform the same behaviours, and also how orangutans utilising different habitats from that observed in this study (i.e. swamp forest) compare. Further studies comparing the ways in which the other non-human apes perform the same arboreal behaviours as orangutans, together with further micro-architecture data from key muscles, would reveal to what extent their positional behaviour repertoires also overlap at a more subtle level, or whether their variation in morphology and behaviour in relation to the environment is more far reaching that previously thought.

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Appendix I. Raw hindlimb data from subjects dissected for present study

Subject	PtamL			PtamR			Ppam		
Muscle	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**
Gluteus maximus	404.0	11.6	32.9	400.3	9.0	42.0	197.1	10.9	17.1
Gluteus medius	380.0	9.0	39.8	380.0	9.0	39.8	292.1	10.1	27.3
Gluteus minimus							35.6	5.9	5.7
Scansorius	-*	-	-	-	-	-	-	-	-
Adductor magnus	102.8	19.6	42.4	854.2	19.0	41.0	336.8	20.8	15.3
Adductor longus	56.0	12.8	4.1	53.0	13.0	3.9	46.5	8.8	5.0
Adductor brevis	42.7	10.5	3.8	48.2	8.0	5.7	40.7	9.4	4.1
Pectineus	24.7	9.1	2.6	-	-	-	16.6	6.4	2.5
Rectus femoris	107.2	7.5	13.5	107.8	7.4	13.7	94.6	9.4	9.5
Vasti	557.2	7.7	68.0	721.3	7.9	86.7	466.0	8.7	50.5
Sartorius	80.8	29.0	2.6	74.7	28.0	2.5	55.4	32.6	1.6
Gracilis	187.7	22.5	7.9	178.4	22.7	7.4	132.0	22.8	5.5
Biceps femoris (long head)	114.8	16.9	6.4	125.7	14.3	8.3	107.5	16.6	6.1
Biceps femoris (short head)	62.4	10.0	5.9	263.1	8.5	29.2	41.5	11.6	3.4
Semimembranosus	157.0	12.7	11.7	156.0	9.8	15.1	274.3	18.3	14.8
Semitendinosus	100.0	19.7	4.8	100.7	12.9	7.4			
Gastrocnemius lateralis	201.4	7.0	27.1	193.2	-	-	52.4	3.9	12.7
Gastrocnemius medialis							82.1	6.8	11.4
Soleus	126.9	3.3	36.3	-	-	-	147.6	5.3	26.3
Plantaris	10.0	7.7	1.2	-	-	-	2.7	4.2	0.6
Popliteus	31.5	3.5	8.5	-	-	-	22.5	3.4	6.3
Tibialis posterior	91.9	2.1	41.3	-	-	-	59.5	3.7	15.2
Tibialis anterior	65.8	6.6	9.4	-	-	-	76.4	11.2	6.5
Flexor hallucis longus	99.1	6.0	15.6	-	-	-	78.7	6.3	11.8
Flexor digitorum longus	45.0	6.1	7.0	-	-	-			
Flexor digitorum fibularis	-	-	-	-	-	-	-	-	-
Extensor hallucis longus	90.0	8.5	10.0	-	-	-	10.3	3.2	3.0
Extensor digitorum longus	33.8	8.5	3.8	-	-	-	33.1	9.1	3.4
Peroneus longus	66.7	5.8	10.9	-	-	-	50.6	4.1	11.6
Peroneus brevis	27.4	5.3	4.9	-	-	-	28.2	3.2	8.3
Piriformis	-	-	-	-	-	-	-	-	-
Obturator externus	-	-	-	38.9	9.3	4.0	-	-	-
Obturator internus	-	-	-	-	-	-	-	-	-
Gemellus inferior	-	-	-	-	-	-	-	-	-
Quadratus femoris	-	-	-	-	-	-	-	-	-
Adductor hallucis	27.5	9.1	2.9	28.2	8.9	3.0	-	-	-
Extensor digitorum brevis	7.6	2.9	2.5	-	-	-	-	-	-
Extensor hallucis brevis	5.4	3.8	1.3	-	-	-	-	-	-
Flexor digitorum brevis	11.1	5.4	1.9	-	-	-	-	-	-
Abductor hallucis	29.1	3.9	7.0	-	-	-	-	-	-
Flexor hallucis brevis	7.1	2.2	3.0	-	-	-	-	-	-
Abductor digiti minimi	13.7	2.5	5.2	-	-	-	-	-	-

*refers to data not present, or not dissected out.

Abbreviations: FL = muscle fascicle length; PCSA = muscle physiological cross-sectional area

Appendix I. contd. Raw hindlimb data for subjects dissected for present study

Subject	Gam			Gsm			Oaf		
Muscle	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**
Gluteus maximus	1377.0	12.3	105.6	1816.0	13.8	124.2	299.2	14.9	18.9
Gluteus medius	1724.0	13.9	117.0	1724.0	13.4	121.4	183.6	8.4	20.6
Gluteus minimus	176.0	9.0	18.5	303.0	10.0	28.6	9.3	5.8	1,5
Scansorius	-	-	-	-	-	-	32.6	9.8	3.1
Adductor magnus	856.0	22.0	36.7	1100.0	28.5	36.4	427.3	16.5	24.4
Adductor longus	711.0	31.0	21.6	783.0	23.0	32.1	41.3	9.4	4.1
Adductor brevis	444.0	13.1	32.0	445.0	17.8	23.6	31.4	8.2	3.6
Pectineus	109.0	17.2	6.0	-	-	-	46.1	10.4	4.2
Rectus femoris	360.0	11.6	29.3	397.2	10.1	37.1	75.2	9.8	7.2
Vasti	1626.0	12.9	118.9	2076.1	11.2	175.7	261.3	6.3	39.1
Sartorius	207.0	40.0	4.9	170.1	43.8	3.7	34.3	28.4	1.1
Gracilis	472.0	40.0	11.1	561.4	31.5	16.8	169.4	30.0	5.3
Biceps femoris (long head)	324.0	10.3	29.7	420.0	18.4	29.7	98.2	15.3	6.1
Biceps femoris (short head)	204.0	14.7	13.1	218.0	13.0	13.1	37.6	13.8	2.6
Semimembranosus	189.0	28.5	6.3	350.0	17.0	19.4	124.7	21.4	5.5
Semitendinosus	590.0	36.0	15.5	688.0	16.9	38.4	164.0	13.6	11.4
Gastrocnemius lateralis	162.0	8.4	18.2	448.0	7.5	56.4	34.1	7.9	4.1
Gastrocnemius medialis	277.0	7.6	34.4				53.1	13.8	3.6
Soleus	338.0	6.9	46.2	499.0	4.4	107.0	70.7	6.1	10.9
Plantaris	-	-	-	-	-	-	-	-	-
Popliteus	62.0	5.1	11.5	105.0	10.0	9.9	10.4	4.4	2.2
Tibialis posterior	131.0	3.8	32.5	161.0	4.2	36.2	28.6	3.4	7.9
Tibialis anterior	199.0	7.4	25.4	211.0	10.1	19.7	71.7	9.4	7.2
Flexor hallucis longus	201.0	7.1	26.7	188.0	9.2	19.3	35.2	5.3	6.3
Flexor digitorum longus	90.0	7.6	11.2	84.0	5.5	14.4	53.3	9.4	5.4
Flexor digitorum fibularis	-	-	-	-	-	-	67.8	9.1	7.0
Extensor hallucis longus	39.0	10.2	3.6	33.0	10.0	3.1	9.5	10.4	0.9
Extensor digitorum longus	126.0	9.7	12.3	134.0	9.3	13.6	40.7	13.7	2.8
Peroneus longus	120.0	5.3	21.4	173.0	6.9	23.7	25.3	9.4	2.5
Peroneus brevis	65.0	5.3	11.6	56.0	6.5	8.1			
Piriformis	-	-	-	-	-	-	17.7	6.6	2.5
Obturator externus	-	-	-	-	-	-	37.3	7.5	4.7
Obturator internus	-	-	-	-	-	-	26.5	5.3	4.7
Gemellus inferior	-	-	-	-	-	-	8.4	5.3	1.5
Quadratus femoris	-	-	-	-	-	-	-	-	-
Adductor hallucis	-	-	-	58	13	4.2	-	-	-
Extensor digitorum brevis	-	-	-	-	-	-	-	-	-
Extensor hallucis brevis	-	-	-	-	-	-	-	-	-
Flexor digitorum brevis	-	-	-	-	-	-	-	-	-
Abductor hallucis	-	-	-	-	-	-	-	-	-
Flexor hallucis brevis	-	-	-	-	-	-	-	-	-
Abductor digiti minimi	-	-	-	-	-	-	-	-	-

*refers to data not present, or not dissected out.

Abbreviations: FL = muscle fascicle length; PCSA = muscle physiological cross-sectional area

Appendix II. Raw forelimb data

Subject	PtamL			PtamR			Ppam		
Muscle	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**
Latissimus dorsi	583.0	25.1	21.9	-	-	-	286.5	34.8	7.7
Deltoid	369.5	7.2	48.4	380.5	9.6	37.4	213.1	11.3	17.8
Infraspinatus	26.0	6.4	3.8	156.6	6.3	23.5	74.7	5.8	12.1
Supraspinatus	75.0	4.4	16.1	27.8	5.9	4.5	54.7	5.5	9.4
Teres major	191.0	13.8	13.1	215.3	13.0	15.6	85.7	14.0	5.8
Teres minor	30.0	5.5	5.2	-	-	-	23.9	7.7	2.9
Subscapularis	206.0	6.0	32.4	-	-	-	127.3	6.4	18.8
Coracobrachialis	53.5	4.9	10.3	74.0	5.4	12.9	30.8	6.2	4.7
Biceps brachii	275.0	14.0	18.5	303.4	17.4	16.5	123.6	15.3	7.6
Triceps brachii	400.0	7.4	51.0	433.8	7.1	57.6	327.8	8.9	34.7
Dorsoepitrochlearis	58.0	9.2	6.0	71.2	10.6	6.3	26.5	12.0	2.1
Anconeus	-*	-	-	-	-	-	4.0	3.3	1.2
Brachialis	191.0	12.8	14.1	218.1	4.3	47.9	94.5	9.4	9.5
Brachioradialis	113.0	15.1	7.1	137.0	20.0	6.5	59.1	20.6	2.7
Supinator	52.0	3.4	14.4	-	-	-	36.4	2.9	11.9
Pronator teres	52.0	3.2	15.3	44.9	5.0	8.5	39.8	4.2	8.9
Pronator quadratus	13.0	2.1	5.8	-	-	-	9.2	1.4	6.2
Flexor carpi ulnaris	77.0	4.1	17.7	94.0	3.6	24.6	57.5	3.8	14.3
Flexor carpi radialis	81.0	6.0	12.7	96.8	5.4	16.9	61.5	6.4	9.1
Palmaris longus	8.0	3.1	0.7	10.5	4.7	0.7	8.9	4.0	0.6
Flexor digitorum profundus	208.5	7.0	28.1	171.5	7.1	22.8	120.8	8.3	13.7
Extensor carpi ulnaris	33.0	4.9	6.4	32.1	4.5	6.7	32.4	4.3	7.1
Extensor carpi radialis longus	46.0	15.9	2.7	43.6	11.8	3.5	28.5	3.8	7.1
Extensor carpi radialis brevis	42.0	6.3	6.3	45.5	4.9	8.8	37.2	5.9	5.9
Flexor pollicis longus	-	-	-	51.9	5.7	8.6	-	-	-
Flexor digitorum superficialis	166.0	3.8	41.2	184.0	4.8	36.2	107.8	5.8	17.5
Abductor pollicis longus	28.0	4.6	5.7	66.1	3.7	16.9	29.4	4.0	6.9
Extensor pollicis longus	8.0	6.2	1.2	28.8	4.5	6.0	7.9	4.5	1.7
Extensor pollicis brevis	-	-	-	20.3	3.5	5.5	-	-	-
Extensor digitorum communis	57.0	6.7	8.0	64.4	5.7	10.7	43.5	6.5	6.3
Extensor digiti minimi	10.0	6.2	1.5	13.8	5.3	2.5	6.0	5.9	1.0
Extensor indicis	4.0	4.7	0.8	5.0	12.0	0.5	3.7	4.0	0.9
Trapezius	239.0	10.0	22.6	-	-	-	141.9	12.3	10.9
Rhomboideus major	-	-	-	-	-	-	-	-	-
Rhomboideus minor	-	-	-	-	-	-	-	-	-
Levatator scapulae	-	-	-	-	-	-	-	-	-

*refers to data not present, or not dissected out.

Abbreviations: FL = muscle fascicle length; PCSA = muscle physiological cross-sectional area

Appendix II. contd. Raw forelimb data

Subject	Pp			Gam			Gsm		
Muscle	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**
Latissimus dorsi	466.8	31.4	14.1	1514.0	40.0	35.7	1397.0	39.0	33.8
Deltoid	299.2	10.5	26.9	1893.0	18.1	98.7	1444.0	10.7	132.3
Infraspinatus	112.7	8.1	13.1	483.0	10.7	42.6	482.0	10.9	41.7
Supraspinatus	65.0	4.3	14.4	361.0	5.7	59.8	-	-	-
Teres major	155.4	15.0	9.8	635.0	18.2	32.9	685.0	19.0	34.0
Teres minor	25.4	7.0	3.4	126.0	8.9	13.4	-	-	-
Subscapularis	187.5	6.7	26.5	796.0	15.2	49.4	760.0	9.3	77.1
Coracobrachialis	72.2	6.3	6.5	104.0	9.4	9.1	98.0	5.7	16.2
Biceps brachii	212.4	18.0	11.1	841.0	22.5	35.3	829.4	25.4	30.9
Triceps brachii	459.0	13.5	32.1	1504.0	12.4	113.8	1607.0	12.8	127.4
Dorsoepitrochlearis	32.0	12.5	2.4	78.0	12.4	5.9	94.0	9.0	9.85
Anconeus	9.6	4.0	2.3	19.0	5.2	3.5	-	-	-
Brachialis	164.4	10.1	15.4	561.0	11.7	45.2	640.0	20.5	34.8
Brachioradialis	96.4	16.9	5.3	333.0	26.6	11.8	319.0	27.3	11.0
Supinator	49.8	3.2	14.7	176.0	5.7	29.1	125.0	5.3	22.3
Pronator teres	45.4	3.7	11.5	168.0	7.0	22.6	157.0	6.4	23.1
Pronator quadratus	14.5	3.0	4.6	36.0	3.8	8.9	27.0	4.2	6.1
Flexor carpi ulnaris	58.1	4.9	11.1	199.0	7.8	24.1	243.0	5.1	45.0
Flexor carpi radialis	64.3	9.3	6.6	193.0	8.0	22.8	169.0	7.3	21.8
Palmaris longus	4.9	6.3	0.6	-	-	-	-	-	-
Flexor digitorum profundus	212.6	10.8	18.6	464.0	12.2	52.0	355.0	7.7	43.5
Extensor carpi ulnaris	32.7	6.1	5.1	90.0	7.6	11.2	95.0	6.5	13.8
Extensor carpi radialis longus	40.2	13.6	2.8	76.0	13.6	5.3	94.0	12.1	7.3
Extensor carpi radialis brevis	41.2	6.0	6.5	124.0	8.1	14.4	131.0	7.5	16.5
Flexor pollicis longus	-	-	-	111.0	10.1	10.4	90.0	8.0	10.6
Flexor digitorum superficialis	157.1	7.7	19.4	341.0	9.6	32.1	308.0	6.6	45.4
Abductor pollicis longus	29.6	8.5	3.3	113.0	4.9	21.8	42.0	8.2	4.8
Extensor pollicis longus	8.8	4.7	1.8	47.0	10.9	4.1	23.0	10.7	2.0
Extensor pollicis brevis	12.6	4.4	2.7	-	-	-	61.0	4.5	12.8
Extensor digitorum communis	50.3	6.4	7.5	79.0	8.9	10.7	191.0	7.8	23.1
Extensor digiti minimi	6.1	8.0	0.7	-	-	-	-	-	-
Extensor indicis	5.4	7.0	0.7	8.4	5.3	6.4	-	-	-
Trapezius	154.9	-	-	1096.0	20.6	50.2	1079.0	32.8	31.0
Rhomboideus major	102.8	15.3	6.4	408.0	20.2	19.1	344.0	12.6	25.8
Rhomboideus minor	43.8	6.9	6.0				-	-	-
Levatator scapulae	-	-	-	-	-	-	-	-	-

*refers to data not present, or not dissected out.

Abbreviations: FL = muscle fascicle length; PCSA = muscle physiological cross-sectional area

Appendix II. contd. Raw forelimb data

Subject	Gp			Gj			Gm		
Muscle	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**
Latissimus dorsi	-	-	-	779.7	17.6	41.8	-	-	-
Deltoid	704.8	12.0	55.4	896.7	7.3	116.6	815.0	10.5	73.2
Infraspinatus	-	-	-	399.5	13.1	28.8	-	-	-
Supraspinatus	-	-	-	-	-	-	-	-	-
Teres major	-	-	-	330.3	19.5	16.0	-	-	-
Teres minor	-	-	-	88.5	12.5	6.7	-	-	-
Subscapularis	-	-	-	-	-	-	-	-	-
Coracobrachialis	-	-	-	99.5	4.8	19.5	58.0	8.8	6.3
Biceps brachii	392.4	23.8	15.6	447.6	8.8	48.3	260.0	18.9	13.0
Triceps brachii	946.0	15.1	59.3	1088.2	15.3	67.1	825.0	12.6	61.9
Dorsoepitrochlearis	-	-	-	-	-	-	26.0	8.0	3.1
Anconeus	28.9	10.0	2.7	16.7	8.3	1.9	20.0	6.0	3.1
Brachialis	385.7	17.5	20.8	327.9	6.9	44.6	290.0	12.0	22.8
Brachioradialis	166.9	16.7	9.4	204.2	18.9	10.2	98.0	15.5	6.0
Supinator	108.1	-	-	-	-	-	66.0	4.0	15.6
Pronator teres	110.5	6.7	15.5	90.4	6.0	14.3	82.0	8.2	9.5
Pronator quadratus	36.9	4.0	8.7	-	-	-	20.0	3.0	6.3
Flexor carpi ulnaris	146.9	8.7	15.9	147.9	2.9	47.6	70.0	6.9	9.6
Flexor carpi radialis	122.7	12.5	9.3	119.9	9.6	11.8	82.0	7.7	10.1
Palmaris longus	-	-	-	-	-	-	-	-	-
Flexor digitorum profundus	328.1	12.9	23.9	407.9	13.3	28.9	266.0	9.7	26.0
Extensor carpi ulnaris	72.7	6.0	11.4	70.9	9.8	6.8	34.0	7.0	4.6
Extensor carpi radialis longus	62.1	22.0	2.7	139.7	9.4	14.0	44.0	10.5	3.4
Extensor carpi radialis brevis	128.1	14.7	8.2	-	-	-	56.0	7.8	6.8
Flexor pollicis longus	-	-	-	-	-	-	-	-	-
Flexor digitorum superficialis	197.6	13.8	13.5	252.1	7.6	31.4	152.0	7.0	20.6
Abductor pollicis longus	52.1	6.0	8.2	-	-	-	74.0	5.0	14.1
Extensor pollicis longus	16.1	7.1	2.2	19.1	6.6	2.7	16.0	6.4	2.4
Extensor pollicis brevis	-	-	-	-	-	-	-	-	-
Extensor digitorum communis	121.5	12.1	9.5	155.0	12.3	11.9	148.0	11.3	24.3
Extensor digiti minimi	19.5	8.0	1.7	-	-	-	-	-	-
Extensor indicis	-	-	-	15.9	6.6	2.3	8.0	5.8	1.3
Trapezius	-	-	-	-	-	-	-	-	-
Rhomboideus major	-	-	-	-	-	-	-	-	-
Rhomboideus minor	-	-	-	-	-	-	-	-	-
Levatator scapulae	-	-	-	-	-	-	-	-	-

*refers to data not present, or not dissected out.

Abbreviations: FL = muscle fascicle length; PCSA = muscle physiological cross-sectional area

Appendix II. contd. Raw forelimb data

Subject	Oaf			Ojf			Ojm		
Muscle	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**
Latissimus dorsi	-	-	-	-	-	-	207.1	17.6	11.1
Deltoid	327.8	7.3	42.4	200.0	7.4	25.5	146.2	8.6	16.0
Infraspinatus	128.9	8.3	14.7	43.4	3.8	10.8	89.0	8.0	10.5
Supraspinatus	83.9	5.0	15.8	21.3	3.3	6.1	30.3	7.1	4.0
Teres major	123.3	13.4	8.7	45.0	8.2	5.2	56.1	12.7	4.2
Teres minor	32.4	6.8	4.5	8.3	3.5	2.2	-	-	-
Subscapularis	197.4	6.1	30.5	65.9	4.0	15.6	102.8	5.0	19.3
Coracobrachialis	44.1	5.8	7.2	15.4	3.6	4.1	23.0	5.9	3.7
Biceps brachii	151.3	18.2	7.9	64.5	7.3	7.9	94.1	13.3	7.6
Triceps brachii	329.5	7.3	41.4	93.0	5.1	17.1	163.8	7.0	22.1
Dorsoepitrochlearis	28.7	10.1	2.7	-	-	-	15.0	8.0	1.8
Anconeus	-	-	-	-	-	-	2.5	3.8	0.6
Brachialis	193.5	18.3	10.0	86.5	6.9	11.9	120.7	7.4	15.4
Brachioradialis	201.6	15.3	12.4	74.0	12.1	5.8	112.5	16.3	6.5
Supinator	53.9	3.4	15.0	18.3	2.6	6.7	26.3	4.0	6.2
Pronator teres	40.0	4.6	8.2	18.4	4.6	3.8	32.0	5.5	5.5
Pronator quadratus	10.6	1.9	5.2	-	-	-	-	-	-
Flexor carpi ulnaris	56.8	10.4	5.2	-	-	-	24.5	7.3	3.2
Flexor carpi radialis	54.3	7.8	6.6	15.2	3.2	4.5	25.8	7.5	3.2
Palmaris longus	23.9	8.4	1.3	-	-	-	-	-	-
Flexor digitorum profundus	211.4	13.4	14.9	61.5	7.9	7.4	85.1	9.1	8.8
Extensor carpi ulnaris	39.2	8.2	4.5	5.3	2.4	2.1	13.6	6.0	2.1
Extensor carpi radialis longus	41.0	10.3	3.8	13.2	6.4	2.0	15.9	9.1	1.6
Extensor carpi radialis brevis	42.0	6.6	6.0	13.0	4.5	2.7	23.5	6.5	3.4
Flexor pollicis longus	-	-	-	17.6	4.7	3.5	22.1	9.6	2.2
Flexor digitorum superficialis	110.2	7.0	14.9	63.3	4.8	12.5	73.6	7.3	9.5
Abductor pollicis longus	32.8	5.5	5.6	-	-	-	-	-	-
Extensor pollicis longus	9.8	5.9	1.6	-	-	-	3.4	8.5	0.4
Extensor pollicis brevis	-	-	-	-	-	-	-	-	-
Extensor digitorum communis	63.2	7.9	7.6	20.8	5.2	3.8	26.3	9.5	2.6
Extensor digiti minimi	14.5	5.2	2.6	-	-	-	-	-	-
Extensor indicis	16.8	7.0	2.3	0.9	2.3	0.3	4.1	7.3	0.5
Trapezius	196.0	12.8	14.4	-	-	-	-	-	-
Rhomboideus major	60.1	10.6	5.3	-	-	-	24.6	5.6	4.1
Rhomboideus minor	22.9	13.9	1.6	-	-	-	11.1	4.9	2.1
Levatator scapulae	40.4	12.6	3.0	-	-	-	-	-	-

*refers to data not present, or not dissected out.

Abbreviations: FL = muscle fascicle length; PCSA = muscle physiological cross-sectional area

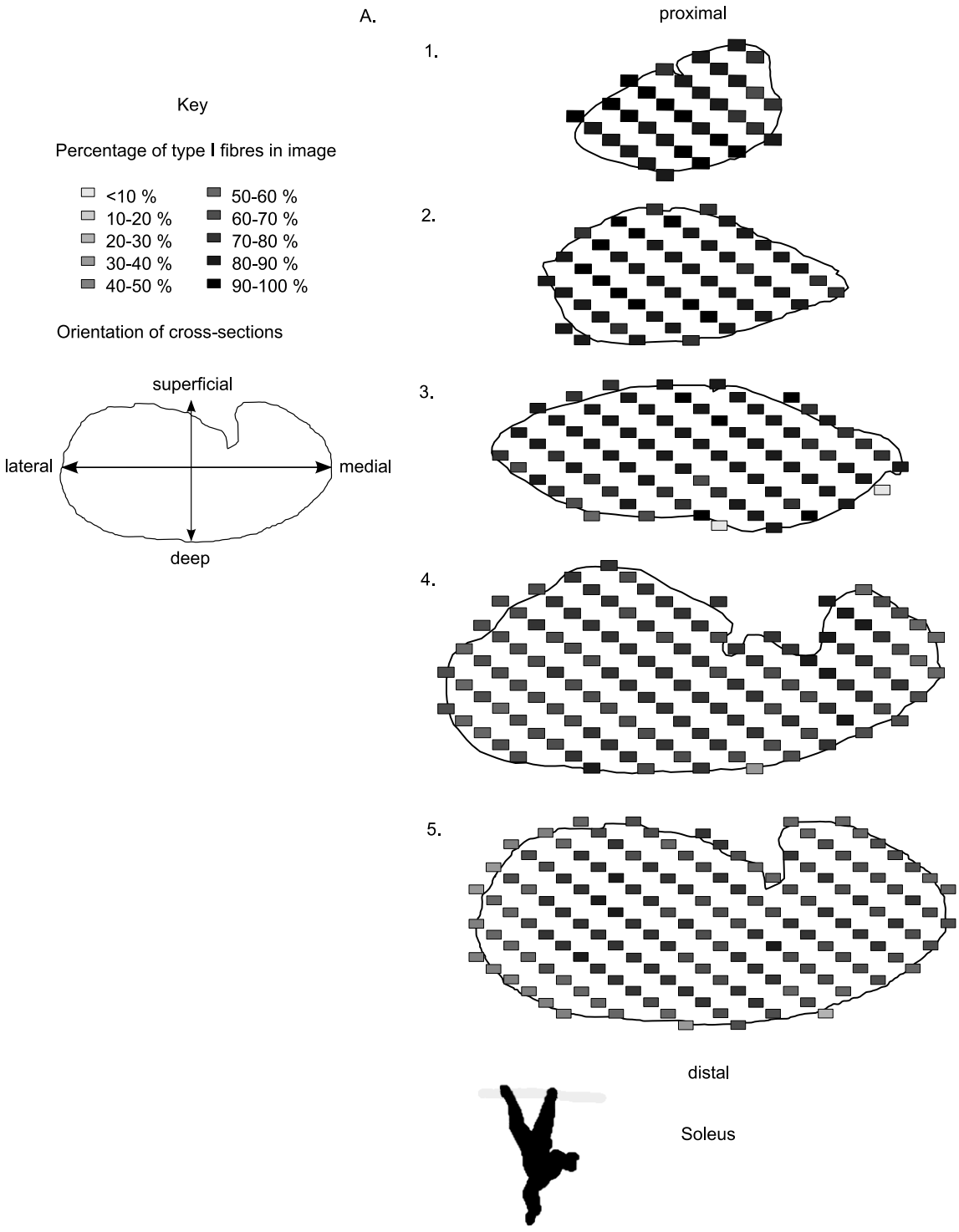
Appendix II. contd. Raw forelimb data

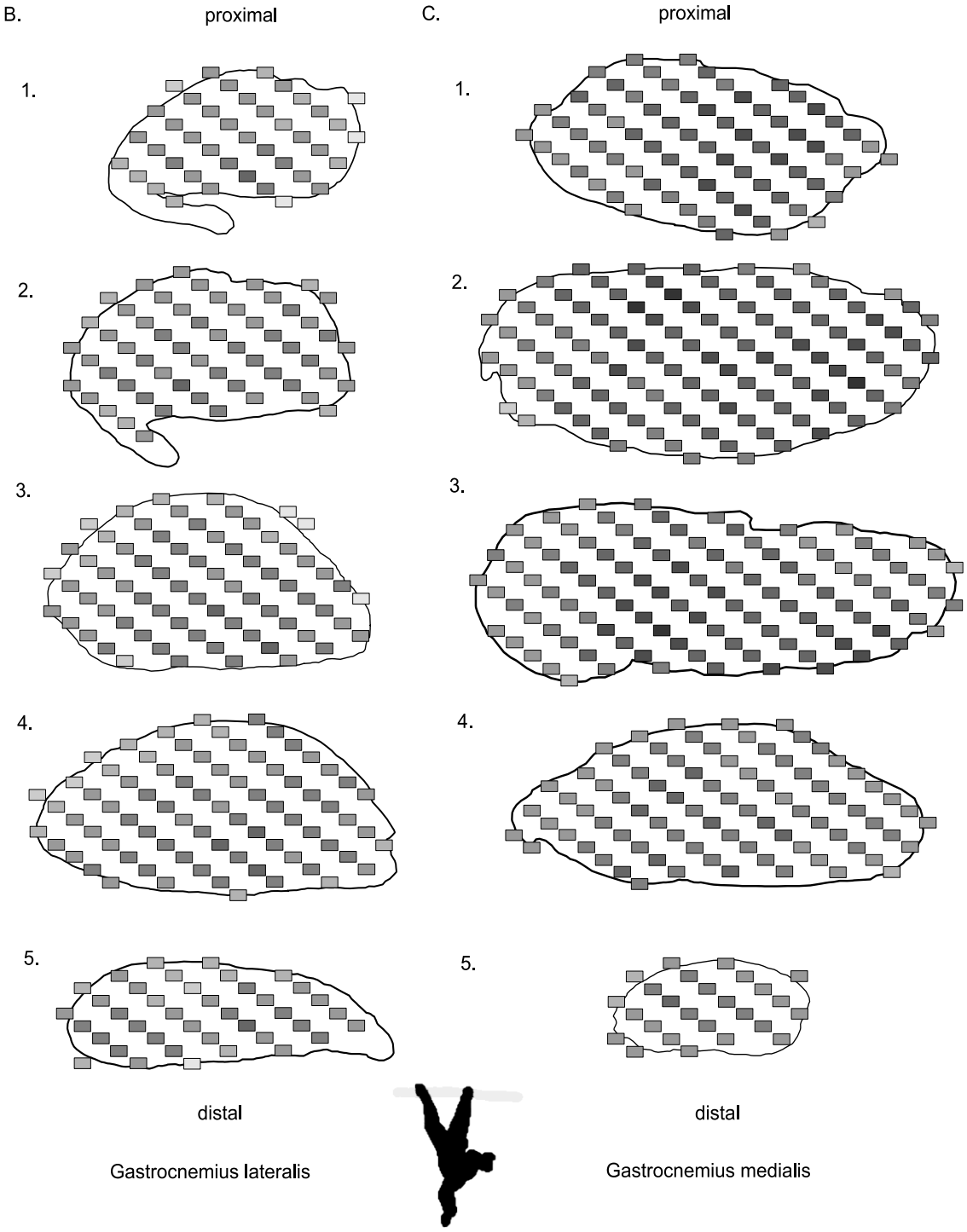
Subject		**Hlf**	
Muscle	**Mass (g)**	**FL (cm)**	**PCSA (cm^2)**
Latissimus dorsi	26.2	7.3	3.4
Deltoid	25.5	3.1	7.8
Infraspinatus	7.3	4.1	1.7
Supraspinatus	4.6	3.2	1.4
Teres major	9.5	5.2	1.7
Teres minor	1.4	3.8	0.4
Subscapularis	13.8	8.0	1.6
Coracobrachialis	2.5	5.5	0.5
Biceps brachii	33.9	7.9	4.0
Triceps brachii	22.5	3.5	6.1
Dorsoepitrochlearis	5.1	6.5	0.7
Anconeus	-	-	-
Brachialis	15.1	5.9	2.4
Brachioradialis	5.2	8.9	0.6
Supinator	3.0	2.3	1.2
Pronator teres	-	-	-
Pronator quadratus	0.5	1.4	0.3
Flexor carpi ulnaris	4.8	1.3	3.5
Flexor carpi radialis	10.2	3.5	2.8
Palmaris longus	3.2	2.5	0.8
Flexor digitorum profundus	22.0	3.4	6.2
Extensor carpi ulnaris	2.1	2.5	0.8
Extensor carpi radialis longus	2.5	5.5	0.4
Extensor carpi radialis brevis	2.7	2.7	0.9
Flexor pollicis longus	-	-	-
Flexor digitorum superficialis	21.0	5.8	3.4
Abductor pollicis longus	4.6	2.5	1.7
Extensor pollicis longus	5.2	-	1.7
Extensor pollicis brevis	-	-	-
Extensor digitorum communis	5.5	3.1	1.7
Extensor digiti minimi	-	-	-
Extensor indicis	2.4	2.5	0.9
Trapezius	13.0	-	-
Rhomboideus major	5.6	4.5	1.2
Rhomboideus minor	-	-	-
Levatator scapulae	-	-	-

*refers to data not present, or not dissected out.

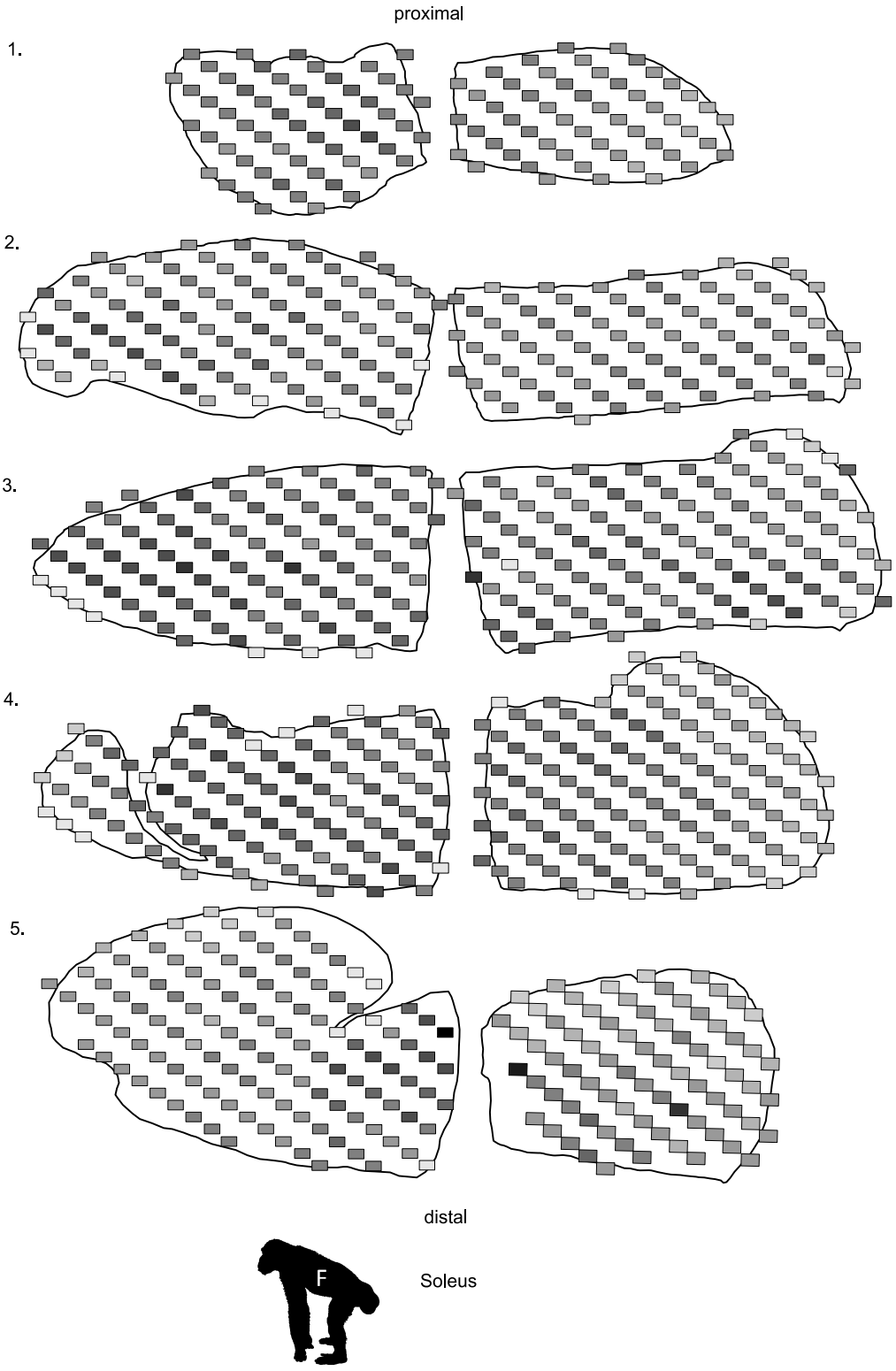
Abbreviations: FL = muscle fascicle length; PCSA = muscle physiological cross-sectional area

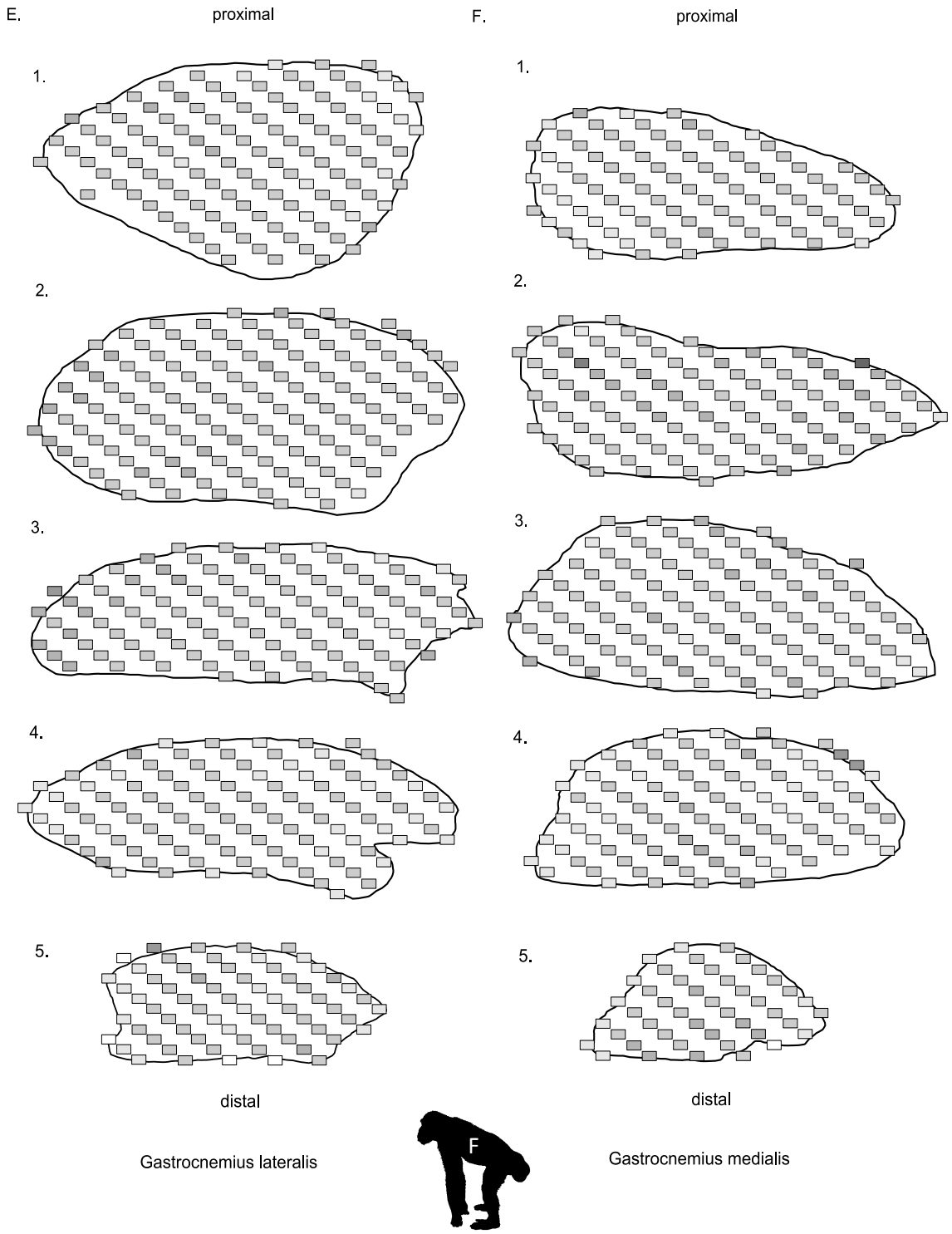
Appendix III. Cross-sections for the five proximo-distal levels showing the percentage of type I fibres in each image counted

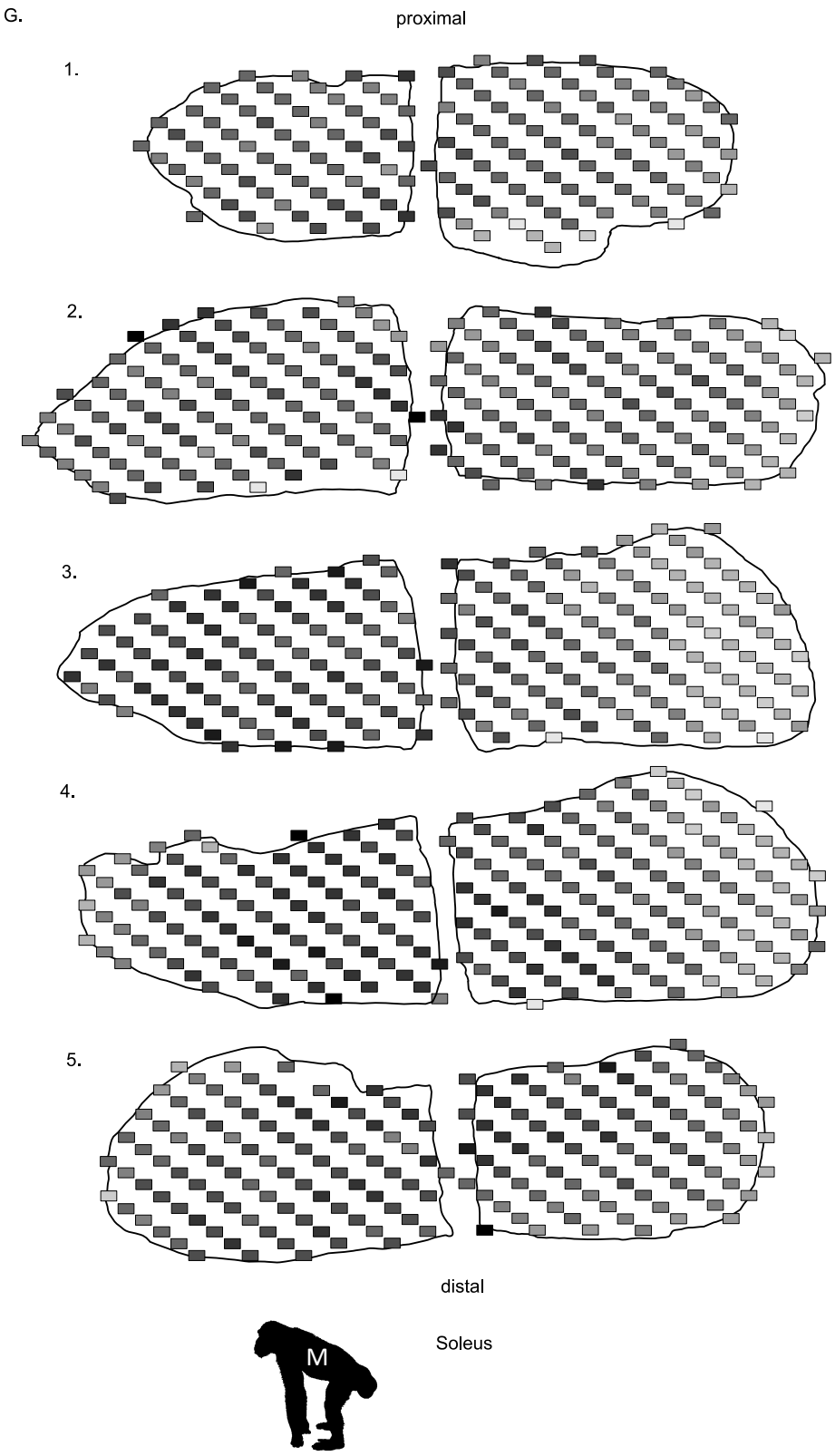


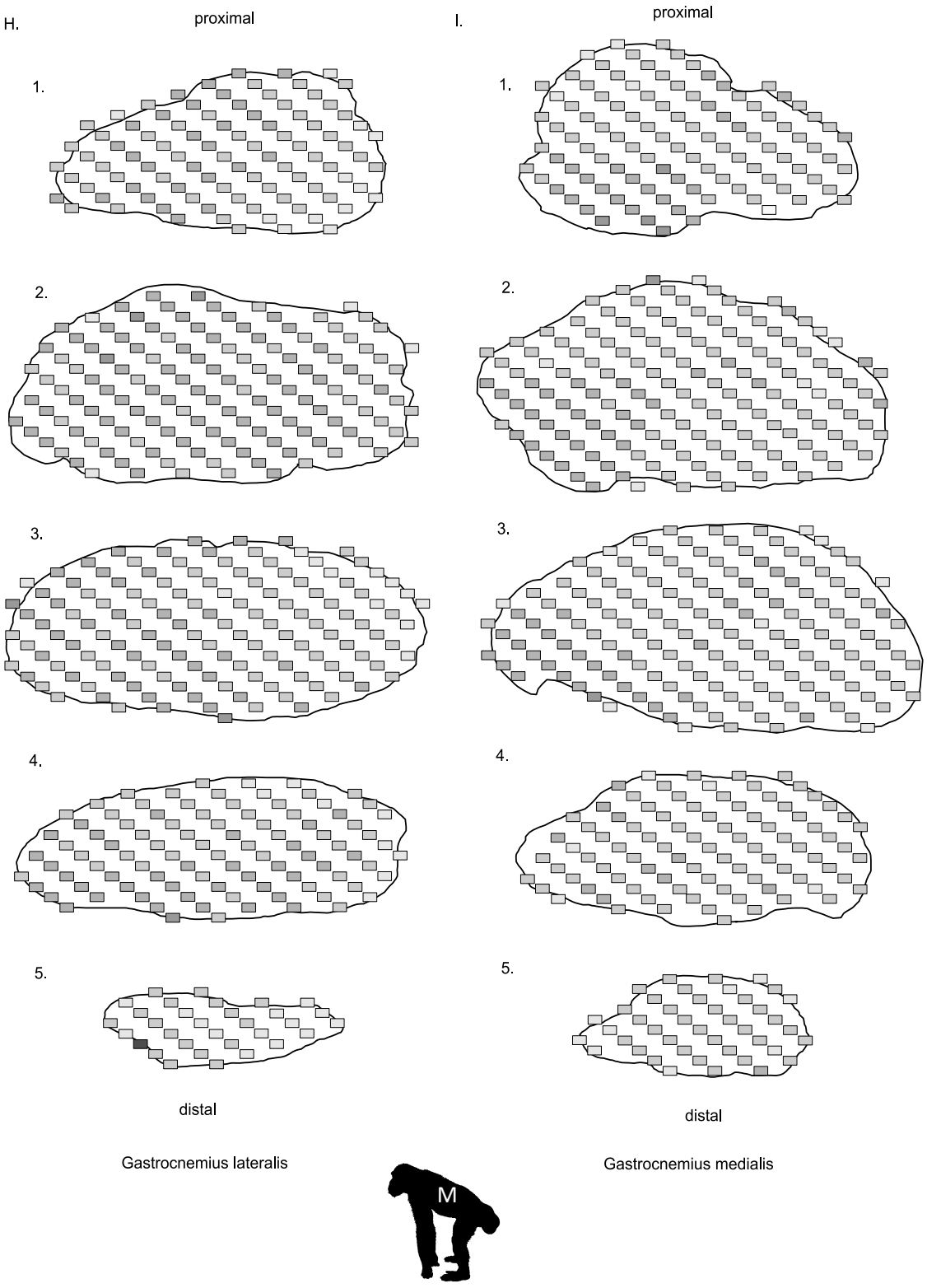

B.
proximal
1.
2.
3.
4.
5.
distal
Gastrocnemius lateralis
C.
proximal
1.
2.
3.
4.
5.
distal
Gastrocnemius medialis

D.




E.
proximal
1.
2.
3.
4.
5.
distal
Gastrocnemius lateralis
F.
proximal
1.
2.
3.
4.
5.
distal
Gastrocnemius medialis
F

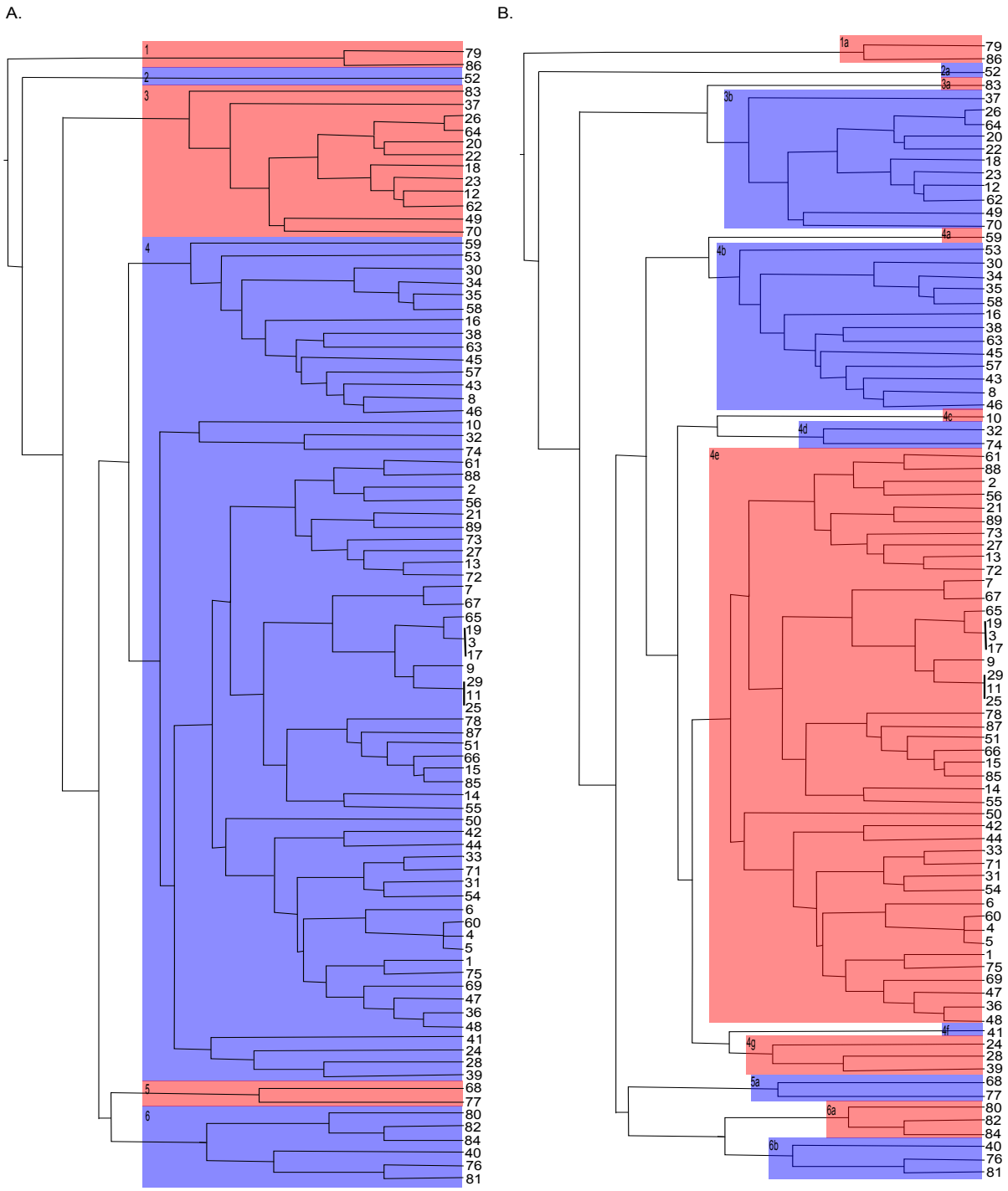

G.
proximal
1.
2.
3.
4.
5.
distal
M
Soleus

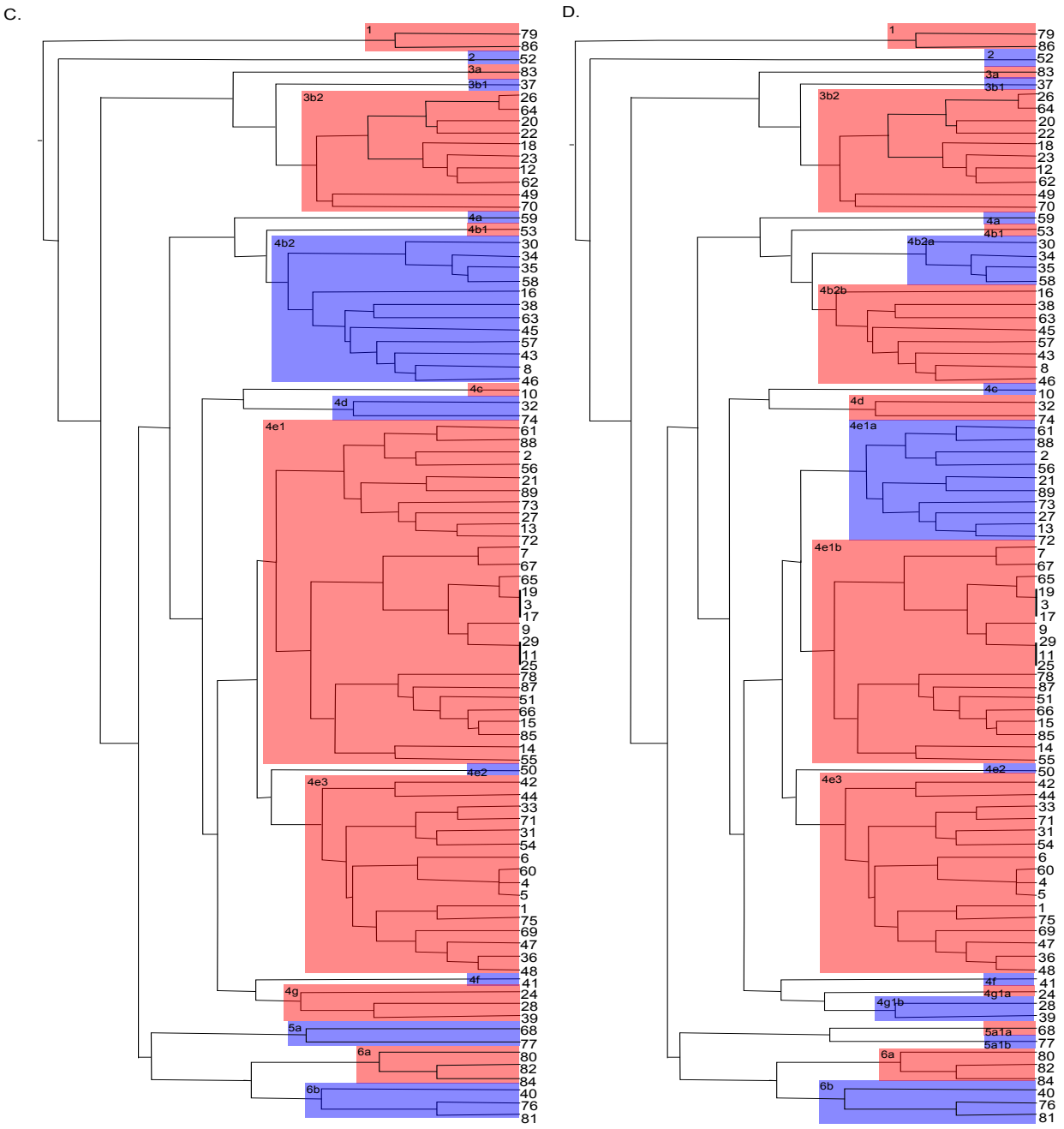


Appendix III. Cross-sections for the five proximo-distal levels (top to bottom) for each muscle showing the percentage of type I fibres in each image counted. Images are only

included for areas where muscle fibres were present, gaps represent areas with no muscle fibres. A. orangutan soleus. B. orangutan gastrocnemius lateralis. C. orangutan gastrocnemius medialis. D. female chimpanzee soleus (each cross-section consisted of two muscle blocks). E. female chimpanzee gastrocnemius lateralis. F. female chimpanzee gastrocnemius medialis. G. male chimpanzee soleus muscle (each cross-section consisted of two muscle blocks). H. male chimpanzee gastrocnemius lateralis. I. male chimpanzee gastrocnemius medialis.

Appendix IV. Dendrograms highlighting relevant groups of postures





Appendix IV. The four dendrograms highlighting the relevant groupings as found from the homogeneity analysis. A. tree 6 (data clustered into six groups), B. tree 14 (data clustered into 14 groups), C. tree 18 (data clustered into 18 groups), D. tree 22 (data clustered into 22 groups). Groupings from tree 6 are labelled 1-6; those in tree 14 are labelled 1a, 1b for example; those in tree 18: 1a1; 1a2 etc and those in tree 22: 1a1a, 1a1b etc as they are broken down into successively smaller clusters.